NEST DEFENCE AS PARENTAL CARE IN THE GREY WARBLER AND THE RIFLEMAN.

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ABSTRACT

Nest defence behaviour, an important component of parental care in birds, was studied in two endemic passerines, the Grey Warbler, *Gerygone igata*, and the South Island Rifleman, *Acanthisitta chloris chloris*, at Kowhai Bush, South Island, New Zealand. Theoretical models based on Triver's parental investment theory predict that parents will increase the risk taken to defend their offspring as offspring age. By testing nest defence response of Grey Warblers and Riflemen to a mounted Little Owl, *Athene noctua*, near the nest I found that both species took a higher level of risk while defending nestlings than eggs. However, I show that the methodology used to study nest defence can affect the results obtained. I repeatedly exposed Grey Warbler and Rifleman parents to the model owl. Their responses after several tests became less intense than for parents that were only exposed to the model once. The level of intensity of nest defence was not affected by either the sex of the parent or whether parents were responding together or alone. Within pairs, Riflemen had highly correlated levels of nest defence response, whereas this correlation was less evident with Grey Warblers. Riflemen were found to adjust their level of defence according to the type of predator threatening the nest. Nest guarding, a previously undescribed aspect of nest defence in male Grey Warblers, was found to be carried out by males only at second nests. I suggest that nest guarding is a response to the threat of brood parasitism by the Shining Cuckoo, *Chrysoccocyx lucidus*.

1. INTRODUCTION AND GENERAL METHODS

INTRODUCTION

In all species of birds, apart from obligate brood parasites, parents actively care for their offspring in some way, for example by incubating eggs and feeding chicks. Parental care is a form of parental investment which was defined by Trivers (1972, p139) as "any investment by the parent in an offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Parent birds need to decide how much they are willing to invest in any one brood and at what cost to themselves. Decision rules to determine the level of parental investment should not be based on past investment which is known as the concorde fallacy (but see Weatherhead 1979), but should be based on the prospective benefits to the parents (Dawkins & Carlisle 1976; Maynard Smith 1977; Sargent & Gross 1985).

Nest defence, an important component of parental care in many birds, involves situations where a parent must immediately decide how much to risk (ie. invest) in its offspring. Following parental investment (PI) theory, nest defence can be defined as "behaviour that decreases the probability that a predator will harm the contents of the nest (eggs or chicks) while simultaneously increasing the probability of injury or death to the parent" (Montgomerie & Weatherhead 1988, p190). This definition allows a cost-benefit analysis of nest defence behaviour.

Before a cost benefit approach to nest defence can be taken, defence behaviour of parents must be shown to be risky at the same time as enhancing nesting success. It could be argued that nest defence is a low risk behaviour as the performer is alert and aware of the predator, but published observations of mobbing birds being captured by predators suggest otherwise (Sordahl 1990a). Both avian and terrestrial predators have been observed to attack and kill mobbing birds (avian: Broun 1947; Denson 1979; Walker 1983; England 1986; Poiani & Yorke 1989, terrestrial: Brunton 1986). Birds responding to one predator may be so intent on mobbing that they are taken by a second, unnoticed predator (Rudebeck 1950, 1951; Southern 1970; Myers 1978). Slagsvold (1982) has reported

that some predators find prey by following mobbing birds.

Observations of nesting Yellow-bellied Sapsuckers, *Sphrapicus varius*, successfully repelling attacks on the nests by hawks and weasels, and of a pair of Veerys, *Catharus fuscenscens*, driving off a garter snake (Petingill 1976) show that it is possible for parent birds to successfully defend their nests against some predators. Evidence that nest defence may positively affect nesting success was first shown by Grieg-Smith (1980) in Stonechats, *Saxicola torquata*, and Andersson et al. (1980) in Fieldfares, *Turdus pilaris*. Blancher & Robertson (1982) found that Eastern Kingbirds, *Tyrannus tyrannus*, that defended their nests more aggressively had a higher nesting success. In colonial-nesting Common Terns, *Sterna hirundo*, colonies that displayed the most aggressive response to a predator showed greater nesting success than less aggressive colonies (Erwin 1988). Aggressive attacks on predators by nesting Northern Jacanas, *Jacana spinosa*, not only reduced predation of nests but also reduced the density of predators near the nest (Stephens 1984). These cases indicate that nest defence accrues benefits in terms of reproductive success to the defending parent.

The intensity of a parent's nest defence response, that is the risk taken to defend the nest, is affected by many different factors such as offspring age, predator type, re-nesting potential, and sex, (for a review see Montgomerie & Weatherhead 1988). Offspring age is expected to positively influence nest defence in parents because as the offspring get older they become more valuable to the parents. Re-nesting potential within a breeding season declines as the season progresses. Nest defence is expected to increase as re-nesting potential declines (Barash 1975). Sex of the defending parent may influence the risk taken to defend the nest according to life history characteristics and the breeding system of each species. The type of predator threatening the nest may also affect the level of risk taken by a parent to defend the nest. The amount of risk that a predator poses to the parents themselves can affect nest defence responses. In this study I investigate how some of these factors affect nest defence in two endemic passerines, the Grey Warbler, *Gerygone igata*, and the South Island Rifleman, *Acanthisitta chloris chloris*.

In Chapter 2 I look at how offspring age affects the pattern of nest defence intensity in the Grey Warbler and the Rifleman and compare my findings to predictions based on PI theory. I also look at how the methodology used to

measure nest defence may affect the results obtained.

In Chapter 3 I investigate whether females and males defend the nest differently and relate this to the social structure of the Grey Warbler and Rifleman.

In Chapter 4 I examine the effect of predator type on nest defence in the Rifleman.

In Chapter 5 I describe nest guarding as part of nest defence by male Grey Warblers and I suggest that nest guarding is in response to brood parasitism by the Shining Cuckoo, *Chrysoccocyx lucidus*.

INTRODUCTION TO THE GREY WARBLER AND THE RIFLEMAN

The Grey Warbler or Rironiro, one of 19 *Gerygone* species distributed throughout Australasia, Indonesia, and the Pacific (Perrins 1990), is endemic to New Zealand. The only other New Zealand member of this group is the Chatham Island Warbler, *Gerygone albofrontata*. *Gerygone* belongs to the suborder Passeri (oscines), parvorder Corvida, superfamily Pardalotidae, subfamily Acanthizinae, and tribe Acanthizini (Sibley et al. 1988).

The Grey Warbler is found throughout the mainland and on offshore islands and is one of the few native, or endemic birds to adapt to the new habitats created by European colonisation. It is found in most types of native forest, coastal areas, swamps, mangroves, exotic plantations, farmland and home gardens, and can be found from sea level up to the subalpine zone (Gill 1985). Adult birds tend to remain in the same locality from season to season as well as from year to year and it is this sedentary characteristic that has allowed most of the Grey Warblers in this study to be banded and their past history known.

Riflemen and Grey Warblers are New Zealand's lightest birds. Male Grey Warblers average 6.5g and females 6.3g (Gill 1980). Plumage is alike in females and males but the sexes can be identified by behaviour. Only males give full song, females rarely sing and give shorter and quieter songs than those of the males. During the pre-lay and laying periods the male guards the female, generally keeping below her most of the time (Cameron 1990).

Grey Warblers are insectivorous. They feed by gleaning insects mainly from the smaller branches and leaves on the outer of the tree (Dean 1989).

The breeding season is from late August to January/February. Pairs are monogamous and remain together outside the breeding season. The female builds an enclosed, dome-shaped nest. The normal clutch size is four and there is an interval of 48 hours between each egg being laid. Incubation is by the female only and takes an average of 19.5 days (Gill 1982a). Both parents feed the nestlings, which fledge at around 17 days old. Grey Warblers are subject to brood parasitism by the Shining Cuckoo, (Gill 1982b).

Grey Warblers are territorial during the breeding season. In autumn territoriality declines and Grey Warblers can often be found in mixed species flocks with Brown Creepers, *Mohoua novaezeelandiae*, Fantails, *Rhipidura fuliginosa*, and Silver Eyes, *Zosterops lateralis*, in Kowhai Bush (Dean 1990).

The Rifleman or Titipounamu is endemic to New Zealand at the infraorder level. Acanthisittides (New Zealand wrens) split away from the suborder Tyranni (suboscines) approximately 80 MYA (Sibley et al. 1988). Two subspecies of Riflemen are recognised, the North Island Rifleman, *A. chloris granti*, and the South Island Rifleman, *A. chloris chloris*. The two have separate geographical distributions and slight differences in colouration and voice (Gray & Gaze 1985).

The Rifleman has survived in a human-modified environment more successfully than its five confamiliarals. The Rock Wren, *Xenicus gilviventris*, is not widely distributed and is possibly endangered. The other three species *Pachyplichas jagmi, P. yaldwini* and *Traversia lyalli* and possibly the Bush Wren, *Xenicus longipes,* are now extinct.

The Rifleman prefers mature native forest but can also be found in second growth native forest (as in Kowhai Bush) and even in mature pine plantations. Riflemen are found in suitable habitats throughout the mainland and on offshore islands. Like Grey Warblers, Riflemen remain in the same location from year to year. The longest recorded movement of a banded bird was less than one kilometre (Gray & Gaze 1985). Even immature birds do not move far from their birth place.

Riflemen are sexually dimorphic in size and plumage. Females are heavier, averaging about 7g whereas males average 5.6g. Females are slightly duller in plumage.

Calls in this species are very simple. A short single "ssip" forms the basis of most calls (Sherley 1985).

Riflemen are insectivorous and up to 94% of their diet overlaps with that of the Grey Warbler (de Hamel 1989), however, the species tend to forage in different niches (McLean & Dean unpubl.).

The breeding season extends from September through to January/February. Like the Grey Warbler, pairs are monogamous and usually remain together between seasons. Both sexes build the nest in a cavity such as a hollow tree or sometimes an empty rabbit burrow. Four or five eggs are laid (approximately 85-92% of the female's body weight) at 48 hour intervals (Sherley 1985). Both sexes share incubation and feeding the chicks. The incubation period is 19 days and the nestling stage lasts for 24 days. Riflemen and Grey Warblers have comparatively longer incubation and nestling stages than their northern hemisphere, ecological counterparts (Sherley 1985). At Kowhai Bush, Riflemen do not appear to be territorial even during the breeding season (Sherley 1985; pers. obs.), although other populations may be territorial (Gray 1969).

GENERAL METHODS

Study site

My study was carried out at Kowhai Bush, a 240ha reserve 8km north-west of Kaikoura township on the east coast of the South Island, New Zealand (N.Z.M.S. 260, 031 605705). The bush is a narrow strip of kanuka/broadleaf forest bordering the north-eastern bank of the Kowhai River. I used two different sites (Fig. 1.1); a 20ha offlying patch surrounded by pasture (site A) and another area within the reserve itself (site B).

Climate and vegetation:

The climate of Kowhai Bush is described in Hunt and Gill (1979). It is characterised by moderate winters and warm summers. Rainfall is fairly evenly

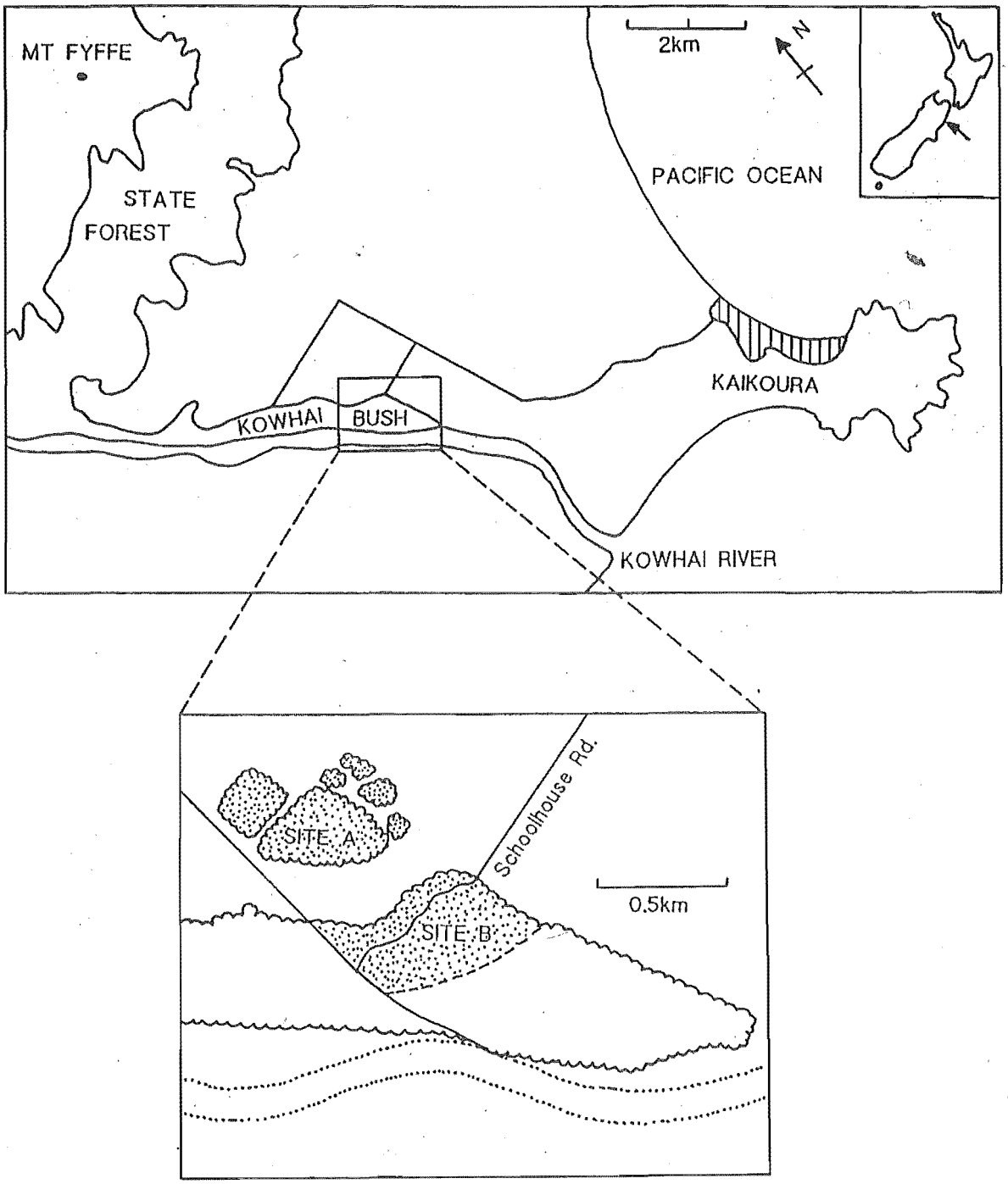

Figure 1.1. Map of the study sites at Kowhai Bush, Kaikoura.

distributed throughout the year, although southerly changes may bring sudden rain, hail, sleet and occasional snow in winter and early spring. The summer period is generally drier, with droughts sometimes brought about by foehn winds from the north-west. Drought conditions were not experienced during the two years of this study.

Dobson (1979) identified 13 different habitat types within the reserve. The areas used in this study cover only two of these:

Habitat 1. Dry stoney soils with a canopy of mainly kanuka, *Kunzea ericoides*. Ground flora is dominated by mosses, lichens, grasses and hook sedges. Site A is periodically grazed by sheep and cattle which keeps undergrowth to a minimum.

Habitat 2. A canopy made up of broad-leaved trees including mahoe,*Melicytus ramiflorus*, and *Coprosma robusta*. An undergrowth of broadleaf saplings and yellow flowering broom, *Cytissus monospessulanus*.

These two habitats were chosen because the trees were generally well spaced giving good visibility and easy access to the nests.

Grid and track system:

Site A is marked out into a 30m x 30m reference grid. A grid marker can be seen from any point within site A allowing easy reference for nest positions. Over 70 Rifleman nest boxes were positioned at grid intersections throughout the site. The grid had been marked out during previous studies on the site.

Site B was marked out by five tracks running parallel through the bush from east to west. Forty-two Rifleman nest boxes were spaced along these tracks.

Adult Identification

The majority of birds in the study areas were individually marked with unique combinations of three colour bands and one individually numbered aluminium band. Grey Warblers were fitted with AA size, plastic, butt-ended, colour bands and AA, butt-ended aluminium, bands. The bottom colour band on each leg was cut down in size and joined with xylene to avoid the bird's claws being caught under the band. The same AA bands were used on Riflemen but colour bands were not cut down.

In the 1989-90 season 93% of male and 20% of female Grey Warblers were banded and at least one of every pair was banded. In the 1990-91 season in site A, 91% of males and 20% of females were banded with only one pair where neither was banded. In site B all seven pairs were un-banded. More males were banded than females as females were rarely caught in mist nets.

In the 1989-90 season 75% of Riflemen were banded and in 93% of all pairs at least one bird was banded. In the 1990-91 season 60% of Riflemen were banded and in 72% of pairs at least one bird was banded. Male and female Riflemen have equal banding rates; most were banded while still in the nest as chicks.

The high proportion of banded birds is due to a banding programme of adults and chicks continued through previous studies in Kowhai Bush since 1976. Banding during this study was carried out under a DOC permit issued to the University of Canterbury.

Finding and monitoring nests

Most Grey Warbler nests were found by following nest building females. Once incubation was initiated it became difficult to locate nests as the female and male become very cryptic. Nests containing nestlings were easier to find as the parents were continually going back and forth to the nest. All Riflemen in the study nested in the nest-boxes provided. Often more than one nest was started by each pair and it was not possible to know which one would be the final nest until the first egg was laid.

Once a nest was found it was monitored every few days. From the information gathered I was able to establish the dates for initiation of incubation, hatching and fledging for all Grey Warbler and Rifleman nests.

Model Tests

The first three sections of my study (Chapters 2, 3 & 4) involve the use of model predators to elicit a nest defence response from parent birds. Models are commonly used in studies of nest defence as they enable the researchers to have more control over their experiments and it is more humane to use models than staged encounters with live predators (Huntingford 1984; Guidelines for the use of animals in research. Anim. Behav. 1991, 41,183-186).

The response of parents to the models were assumed to be similar to their response to a live predator. Several studies have found the response to a model is similar to that of a live predator except, that it may be less intense (Curio 1975; Shalter 1978a).

Recognition of a model as a predator by a bird relies on the triggering of a sign stimulus or releasing mechanism (Curio 1975; Barash 1975). For example certain owl characteristics, such as body shape, eyes and feather detail are important in the recognition of an owl model as a predator (Curio 1975).

The three models I used were realistic taxidermic mounts of a Little Owl, *Athene noctua*, a Ship Rat, *Rattus rattus*, and a Song Thrush, *Turdus philomelos clarkei*. Models were presented to the birds between 1 and 2m from their nests, orientated towards and level with the nest entrance. Models were positioned only after both parents had left the nest area. This procedure was the same for both species and all nesting stages except for tests during Rifleman incubation. At these tests the model had to be positioned while one bird was incubating, as there was not sufficient time to erect the model between one bird leaving the nest and the other bird arriving. The bird on the nest did not appear to be aware of the model prior to leaving the nest. For Grey Warbler tests the models were hoisted to the correct position using a pre-placed string. Models for Rifleman tests were hooked over a branch near each nest.

Data collected during all model tests were recorded onto a hand held mini cassette recorder. Data were transcribed off the tapes the same day they were recorded.

Definitions of terms used in this thesis

First nest: the first clutch of the season for each pair.

Renest: any replacement clutch for one lost due to any reason eg. predation or adverse weather conditions etc.

Second nest: the clutch laid after the fledging of the chicks from the previous nest.

Test: where a model is presented to parent birds outside their nest and their response is recorded for a 2 minute period.

Nest defence intensity: the risk taken by a parent to defend its nest.

2. PATTERNS OF NEST DEFENCE AS OFFSPRING AGE AND METHODOLOGICAL CONSIDERATIONS.

INTRODUCTION

The most consistent pattern found in previous studies of nest defence is an increase in the intensity of the defence response (measured as risk taken by the parent) from egg laying through to fledging (Montgomerie & Weatherhead 1988). This pattern has been found in passerines (Andersson et al. 1980; Grieg-Smith 1980; Patterson et al. 1980; East 1981; Redondo & Caranza 1989) and non-passerines (Barash 1975; Pugesek 1983; Brunton 1990).

Theory

At the ultimate level, a pattern of increasing risk through the nesting cycle has been explained by Triver's (1972) parental investment theory, which is derived from optimality theory. The risk taken to defend the nest (investment by the parent) should increase as expected benefits become greater due to offspring aging. The increasing value of an offspring to the parent as the offspring ages can be explained in two ways: 1) the cost of getting a replacement clutch to the same stage as the present one, increases as the offspring age (Barash 1975), or 2) the relative difference between parent and offspring, in expected future survival, decreases as the offspring age (Andersson et al. 1980). The optimal level of defence still increases with offspring age even when it is not possible to lay a replacement clutch, which suggests that the changing difference between offspring and parent future expected survival may be the driving variable behind increasing levels of nest defence (Andersson et al. 1980).

The optimal nest defence response predicted for altricial species increases gradually from a low level early in incubation as the probability that the eggs will hatch increases (Montgomerie & Weatherhead 1988). The level of defence rises more rapidly after hatching to a peak just before fledging, with a rapid drop after fledging as offspring become more independent (Fig. 2.1a, McLean & Rhodes 1991

taken from Montgomerie & Weatherhead 1988).

A proximal approach to nest defence patterns has been taken by McLean & Rhodes (1991). Their "feedback hypothesis" involves a mechanism based on feedback signals provided by the current young to predict defence levels by parents. The hypothesis predicts a different pattern of nest defence as offspring age than that predicted by optimality theory. The feedback hypothesis predicts a plateau in the defence intensity during incubation, as the stimulus provided by the eggs in the nest is static throughout this period. Hatching produces a step function in the curve due to the increased stimulus provided by moving chicks. Events which change the stimuli that the parents receive from the chicks such as growth, begging calls and the irruption of feathers, influence the shape of the curve after hatching (Fig 2.1b, from McLean & Rhodes 1991).

McLean & Rhodes provide some evidence in support of their hypothesis but clearly more data are needed for it to be convincing. If the feedback hypothesis is shown to be a useful tool for understanding nest defence in birds then it could be used in two ways: (1) Optimality theory and the feedback hypothesis are not mutually exclusive. As pointed out by McLean & Rhodes, the feedback hypothesis may be the most efficient mechanism available to parents for gauging the optimal nest defence level that has evolved so far. (2) As nest defence is made up of a number of different behaviours and is affected by many different factors, these proximate factors may have a stronger influence on the nest defence response of a bird in a given situation than natural selection. If this is the case then the feedback hypothesis may be more useful for predicting defence levels than Optimality Theory.

Methodological considerations

Not all studies of nest defence have found an increase in defence intensity as offspring age. Many previous studies have repeatedly tested the same parent birds every few days throughout the breeding season. Knight & Temple (1986a) proposed that by repeatedly testing at the same nests researchers were influencing the defence response of parent birds through positive reinforcement and loss of fear. Using nests tested only once, Knight & Temple (1986a,b) found no increase in the defence

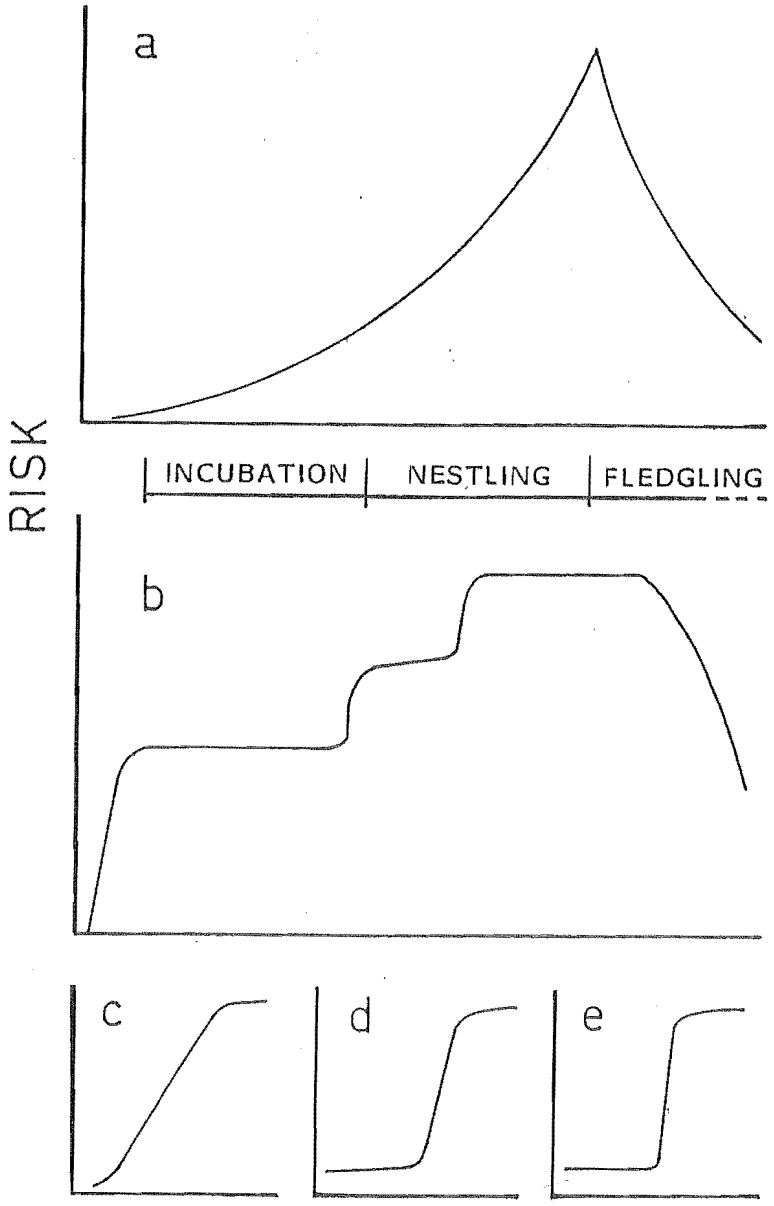

Figure 2.1. Nest defence response curves in terms of risk during the breeding cycle predicted by optimality theory (a, Montgomerie & Weatherhead 1988), and by the feedback hypothesis (b, McLean & Rhodes 1991). The nestling component of the feedback hypothesis curve is made up of a combination of curves for growth (c), volume of nestling begging calls (d), and first appearance of juvenile plumage (e).

intensity for three passerine species, but at nests tested repeatedly nest defence did increase as the offspring age. Hobson et al. (1988) tested Yellow Warblers only once and also found no increase in defence intensity.

However, subsequent studies on Song Sparrows, *Melospiza melodia*, (Weatherhead 1989), Indigo Buntings, *Passerina cyanea*, (Westneat 1989) and Willow Tits, *Parus montanus*, (Rytkonen et al. 1990) found that repeated testing did not affect nest defence responses. It is possible that different species respond to repeated testing differently.

The nest defence behaviours chosen to be measured by researchers may also affect the results obtained, as some behaviours may be better indicators of the risk taken by the parent than others. Some studies of nest defence have relied entirely on call types and call rates (Grieg-Smith 1980; East 1981; Knight & Temple 1986c). Calls are only one part of the nest defence response in most species and so measuring calls alone may not give an accurate indication. Other studies have included behaviours such as measures of distance of the parent from the predator, number of flights, swoops etc. Care must be taken when deciding which behaviours to use to measure a nest defence response.

Predictions

In this chapter I investigate the pattern of nest defence as offspring age in the Grey Warbler and the Rifleman. In some species it is difficult to separate the effects of offspring age and renesting potential. Grey Warblers and Riflemen are double brooded but cannot raise more than two broods in a season. I tested nest defence responses to a Little Owl, *Athene noctua*, through the incubation and nestling stages at first nests of both species. Through this period renesting potential did not significantly decrease as all pairs had time available to renest successfully if the first nest failed. Therefore, the pattern of nest defence obtained in this study was most likely due to the effects of offspring aging.

I also look at the methodology used to study nest defence patterns. I determined whether repeatedly testing the same parents affected nest defence response in Grey Warblers and Riflemen by comparing nest defence responses of parents that have been

repeatedly exposed to the Little Owl model with responses of parents that had not been tested with the Little Owl model before. I review behaviours which have been used to measure nest defence in previous studies and discuss how accurately these behaviours reflect the level of risk taken by the parent to defend its offspring.

METHODS

Model tests were used to induce a nest defence response at first nests of Grey Warblers and Riflemen at Kowhai Bush, Kaikoura. Data were collected during the 1989-90 and 1990-91 breeding seasons. Nests tested in the second season belonged to different pairs to those tested in the first season.

The Model

The model chosen needed to have two specific properties. First, the species used should not be common in the study area so the parents' exposure to the model during the testing period was essentially limited to the tests. Second, the model must be recognised by the parents as a real threat to both the nest and themselves. The Little Owl (Fig 2.2.) was chosen as an appropriate predator for the model experiments as it fits the properties required of the model. This species was introduced to New Zealand from Germany in 1910 in the hope that it would control small passerines in orchards (Morse 1985). Although the Little Owl is present in the Kaikoura region it prefers a pastoral habitat and does not venture into forest or bush. It may hunt along the edges of bush, but it is unlikely that forest-nesting birds would be exposed to the Little Owl during the breeding season. The Little Owl is mainly an insectivore but also preys on frogs, lizards, mice and small passerines, especially while nesting (Rule 1977; Morse 1985). The behaviour of Grey Warblers and Riflemen towards the model indicated that the Little Owl was perceived as a real threat (pers. obs.)

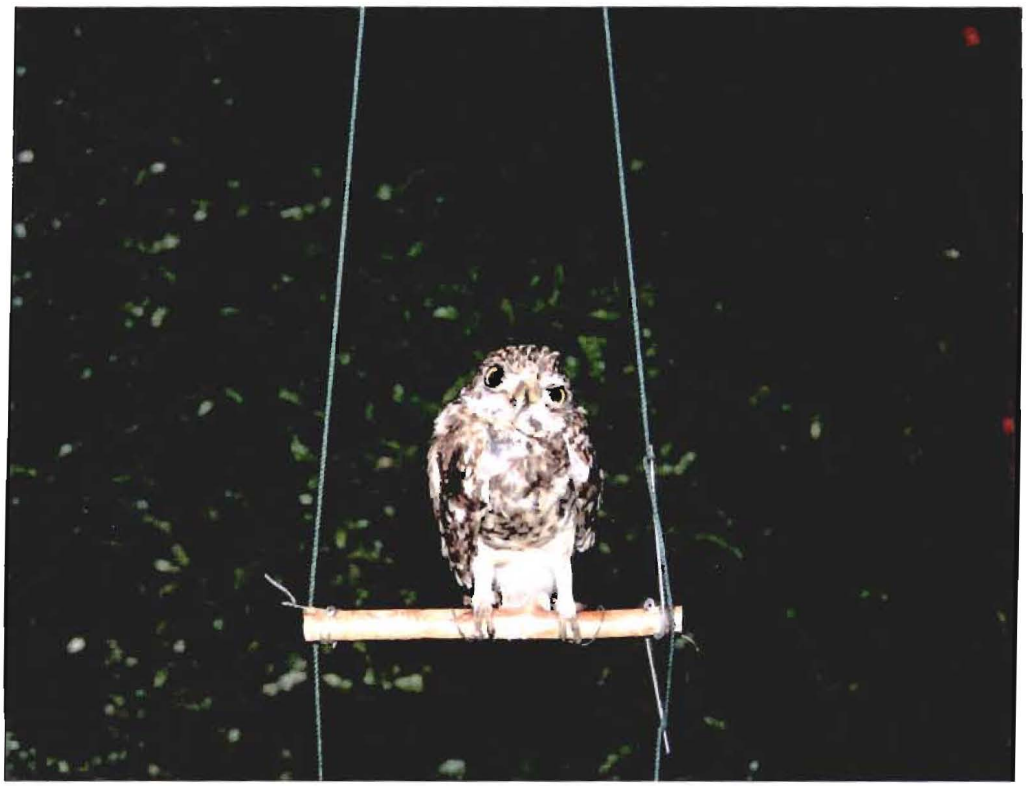

Figure 2.2. Model of the Little Owl, *Athene noctua*.

Procedure

Before testing, the 23 Grey Warbler and 30 Rifleman first nests were assigned to one of the following categories:

1. Nests tested with the model only once during the incubation stage.
2. Nests tested with the model only once during the nestling stage.
3. Nests tested with the model every three days throughout the incubation and nestling stages.

During a test the model was presented to the birds as described in Chapter One. The model was presented between one and two metres from the nest (GW $\bar{x}$=1.62m, RF $\bar{x}$=1.58m) while the parents were not in the area. Once one or both parents has returned to the nest and saw the model, their behaviour and distance from the model was recorded for two minutes (see below for behaviours recorded). The model was then removed from sight and the birds were watched until incubation was resumed or the chicks were fed. All tests were carried out between 0800 and 1200 hours.

Behaviours recorded

I recorded three measures of the distance of the parent from the model during the test period:

Minimum distance (m) - an estimate of the closest approach of a parent to the model.

Maximum distance (m) - the greatest distance of the parent from the model.

Mean distance (m) - calculated using the average of 12 estimates of the parents' distance from the model obtained from instantaneous samples taken at 10 second intervals throughout the test period.

Intensity score - calculated from the type of behaviours used during a test (Table 2.1). A value from 1 (low intensity) to 5 (high intensity) was calculated for each bird at each test. The intensity score gives an indication of the overall risk taken by a parent.

All calls were recorded during the test and analysed as the number of calls per minute. Call types differed depending on which species was being tested.

Grey Warblers: Rate of singing and alarm calling - the number of songs include

Table 2.1. Intensity score categories for Grey Warblers and Riflemen.

Intensity	Grey Warbler	Rifleman
1	No interest shown in the model, parent incubates or feeds chicks.	No interest shown in the model, parent incubates or feeds chicks.
2	Avoids nest, little activity, no calling, >2m from the model.	Avoids nest, little activity, maybe some low intensity calls, >2m from the model.
3	Not to nest, more activity, some song, >1m from the model.	Avoids nest, more activity, low intensity calls, >1m from the model.
4	Avoids nest, some song and alarm calls, <1m but >0.5m from the model	Avoids nest, low intensity threat calls, <1m from the model but >0.5m.
5	Not to nest, lots of song and alarms, maybe some swoops, <0.5m from the model.	Not to nest, down trills, may be swoops or wing raises, <0.5m from the model.

full song and sub-song. Calls were analysed as the number of calls per minute.

Riflemen: Low intensity alarm calls - a run of single "ssip" calls in staccato fashion. As these calls were often rapid the number of calls was not counted. The amount of low intensity calling in a test was ranked on a three point scale: 1 = less than 20 calls, 2 = more than 20 calls but not continuously calling, 3 = continuous low intensity calls.

Down trill - the longest and most complicated Rifleman call, consisting of a series of short notes run together starting at a high frequency and rapidly dropping to a sustained note (Sherley 1985). It is the most intense alarm call. Down trills were analysed as the number of trills per minute.

Analysis

When both parents attended a test, both of their responses were recorded. Only the most intense response was used in the analysis.

Data from nests that were repeatedly tested were analysed using a linear regression analysis. Where Mann-Whitney U tests were used all P values reported are 2-tailed unless otherwise specified.

RESULTS

Patterns of nest defence at nests that were tested repeatedly:

Nest defence responses from Grey Warbler nests that had been tested repeatedly (n = 10) showed a slight but significant positive relationship between the stage of the nesting cycle and mean distance of the parent from the model when tested using a linear regression analysis (Table 2.2). A linear regression of tests conducted during incubation only, revealed a small positive relationship with mean distance and a small negative relationship with intensity score (Table 2.3). A similar analysis for the nestling stage only showed significant positive relationships for the intensity score and the song rate (Table 2.4).

Table 2.2. Grey Warblers: Linear regression analysis of nest defence measures in relation to the day of the nesting cycle for 10 nests that were tested repeatedly at 3 days intervals (R^2=regression coefficient).

Behaviour	R^2	p
Minimum distance (m)	0.0208	NS
Maximum distance (m)	0.0300	0.07
Minimum distance (m)	0.0415	<0.05
Intensity level	-0.0069	NS
Song (no./min.)	0.2289	<0.0001
Alarm (no./min.)	0.0408	<0.05

Table 2.3. Grey Warblers: Linear regression analysis of nest defence measures in relation to the day of the incubation stage for 10 nests that were tested repeatedly at 3 day intervals (R^2=regression coefficient).

Behaviour	R^2	p
Minimum distance (m)	0.0725	NS
Maximum distance (m)	0.0739	NS
Mean distance (m)	0.1076	<0.05
Intensity level	-0.0878	<0.05
Song (no./min.)	-0.0284	NS
Alarm calls (no./min.)	0.0043	NS

Table 2.4. Grey Warblers: Linear regression analysis of nest defence measures in relation to day of the nestling stage for 10 nests that were tested repeatedly at 3 day intervals (R^2=regression coefficient).

Behaviour	R^2	p
Minimum distance (m)	0.0027	NS
Maximum distance (m)	-0.0234	NS
Mean distance (m)	-0.0092	NS
Intensity level	0.1428	<0.01
Song (no./min.)	0.4231	<0.0001
Alarm calls (no./min.)	-0.0115	NS

The pattern of the intensity score for Grey Warblers as the nesting cycle progresses showed a decreasing intensity through the incubation period and then a stepped pattern of increase through the nestling stage (Fig. 2.3).

Linear regression analysis of repeatedly tested Rifleman nests (n=9) showed no significant relationship between the stage of the nesting cycle and any of the behaviours measured except for mean distance (Table 2.5). There were no significant relationships for stage of incubation for any of the variables (Table 2.6) and only low intensity calls were significant for the nestling stage (Table 2.7).

The pattern of the intensity score for Riflemen parents as the nesting cycle progresses showed a slight decrease in intensity through the incubation period and a stepped increase immediately after hatching (Fig.2.4), after which intensity remained fairly constant throughout the nestling stage.

The few significant results from the linear regression analysis explained only a small proportion of the variation in the data and were not always consistent in the direction of difference. Therefore, I averaged scores from each nest for each behaviour in order to compare overall responses at the incubation and nestling stages. Incubation and nestling scores for each behaviour were compared using Wilcoxon signed rank tests for matched pairs. Grey Warblers (n=10) sang more during the nestling stage ($p<0.05$, 1 tailed) but alarm called less ($p<0.05$, 1 tailed). None of the other behaviours measured, including overall intensity score, were significantly different between the two nesting stages (Fig. 2.5). The measures of distance tended to become less intense at the nestling stage (Fig. 2.5) For Riflemen (n=9), a significant increase in intensity from the incubation to the nestling stages was found for intensity score ($p<0.05$, 1 tailed), and down trills ($p<0.05$, 1 tailed). All the remaining behaviours showed a trend towards increased intensity at the nestling stage (Fig 2.6).

Nests tested only once during incubation or nestling stages:

For Grey Warblers there was a significant increase in the risk taken to defend the nest between the incubation stage and the nestling stage, indicated by an increase in the number of songs ($p<0.05$, 1 tailed) and the number of alarm calls

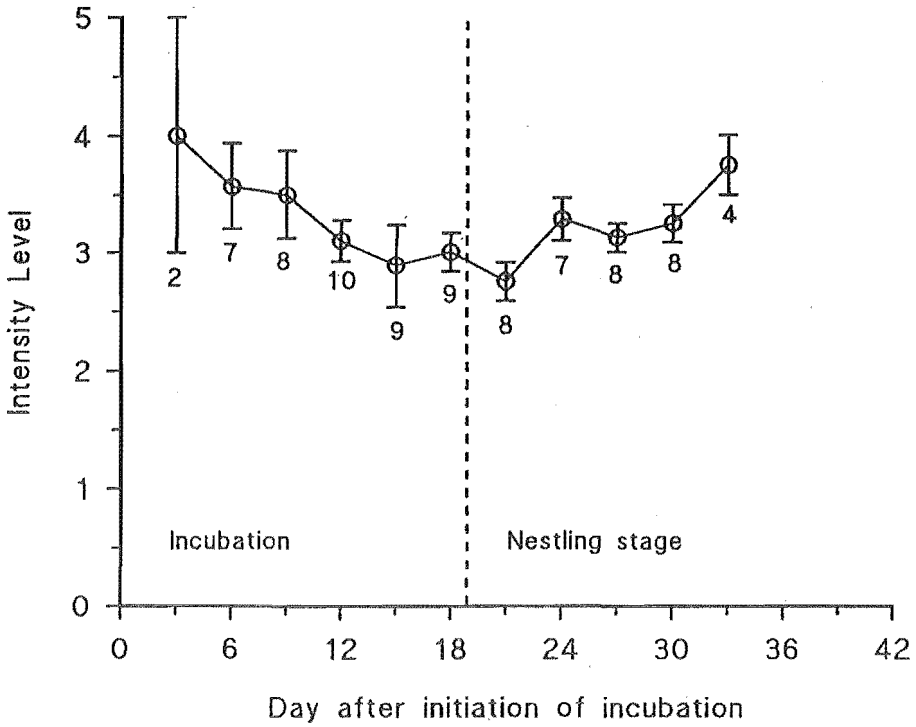

Figure 2.3. Pattern of intensity score at Grey Warbler nests tested repeatedly at 3 day intervals (mean ± SE, numbers under the graph indicate sample sizes).

Table 2.5. Riflemen: Linear regression analysis of nest defence measures in relation to day of the nesting cycle for 9 nests that were tested repeatedly at 3 day intervals (R^2=regression coefficient).

Behaviour	R^2	p
Minimum distance (m)	-0.0085	NS
Maximum distance (m)	0.0088	NS
Mean distance (m)	0.0299	<0.05
Intensity level	0.0199	NS
Low int. calls (no./min.)	0.0120	NS
Down Trills (no./min.)	0.0259	0.06

Table 2.6. Riflemen: Linear regression of nest defence measures in relation to day of the incubation stage for 9 nests that were tested repeatedly at 3 day intervals (R^2=regression coefficient).

Behaviour	R^2	p
Minimum distance (m)	-0.0089	NS
Maximum distance (m)	-0.0052	NS
Mean distance (m)	-0.0186	NS
Intensity level	0.0291	NS
Low int. calls (no./min.)	-0.0243	NS
Down trills (no./min.)	-0.0055	NS

Table 2.7. Riflemen: Linear regression analysis of nest defence measures in relation to day of the nestling stage for 9 nests that were tested repeatedly at 3 day intervals (R^2=regression coefficient).

Behaviour	R^2	p
Minimum distance (m)	-0.0069	NS
Maximum distance (m)	-0.0011	NS
Mean distance (m)	0.0174	NS
Intensity level	-0.0120	NS
Low int. calls (no./min)	0.0729	<0.05
Down trills (no./min.)	-0.0046	NS

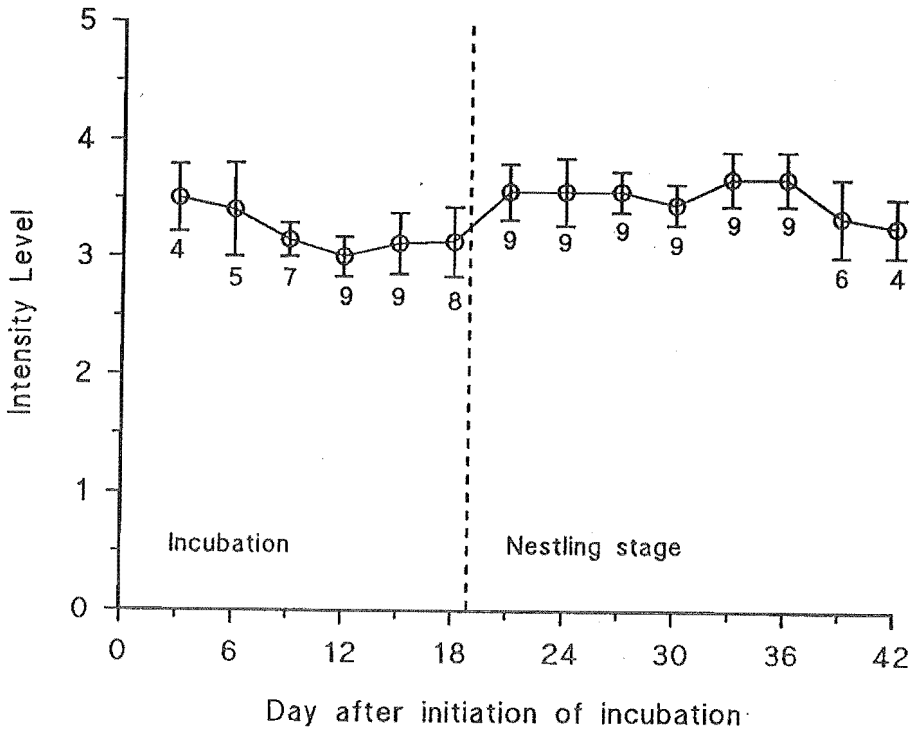

Figure 2.4. Pattern of intensity score at Rifleman nests repeatedly tested at 3 day intervals (mean ± SE, numbers under the graph indicate sample sizes).

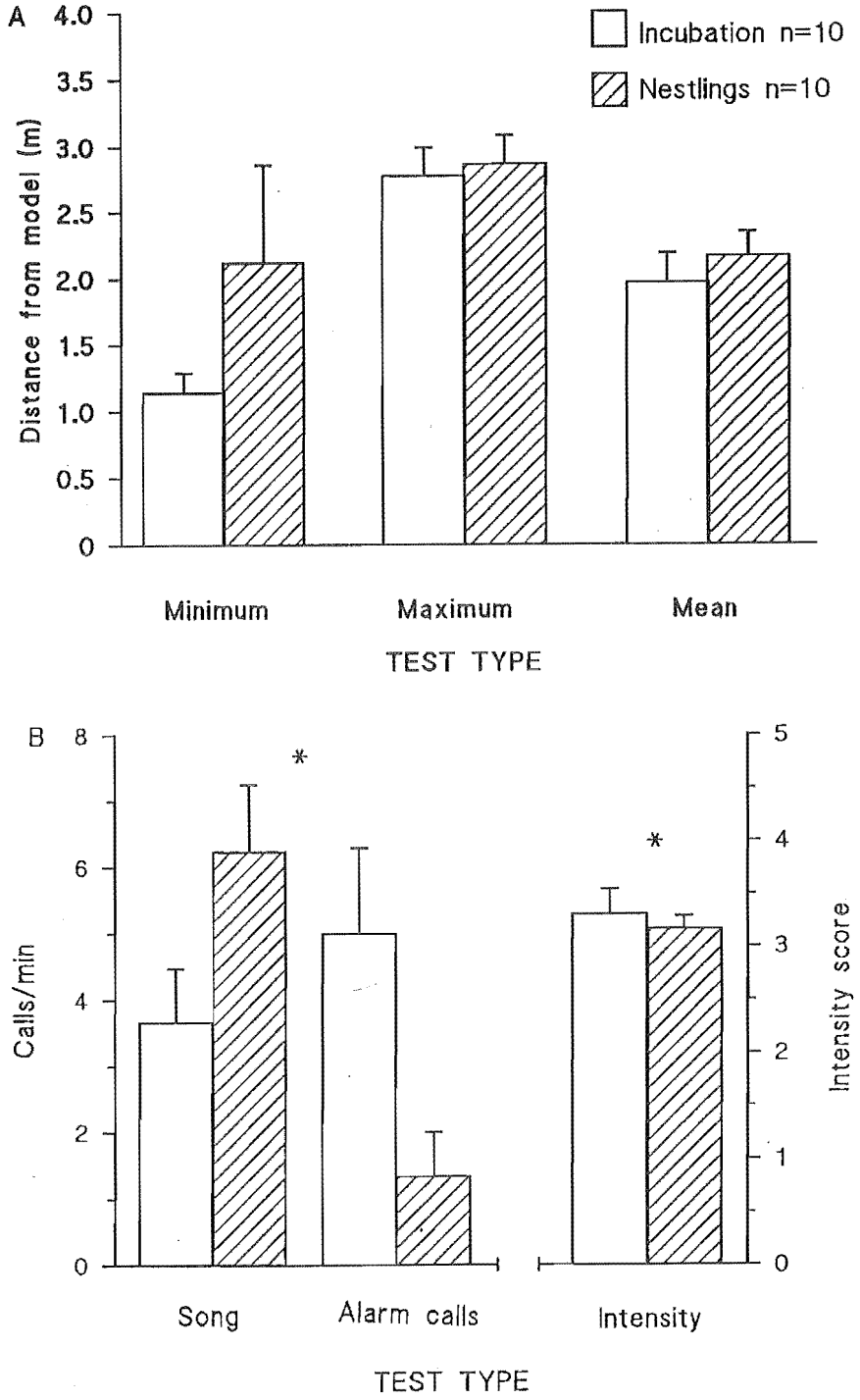

Figure 2.5. Comparison of average nest defence measures for Grey Warbler nests tested repeatedly at 3 day intervals at the incubation and nestling stages (Wilcoxon sign rank test, mean ± SE, * = $p < 0.05$).

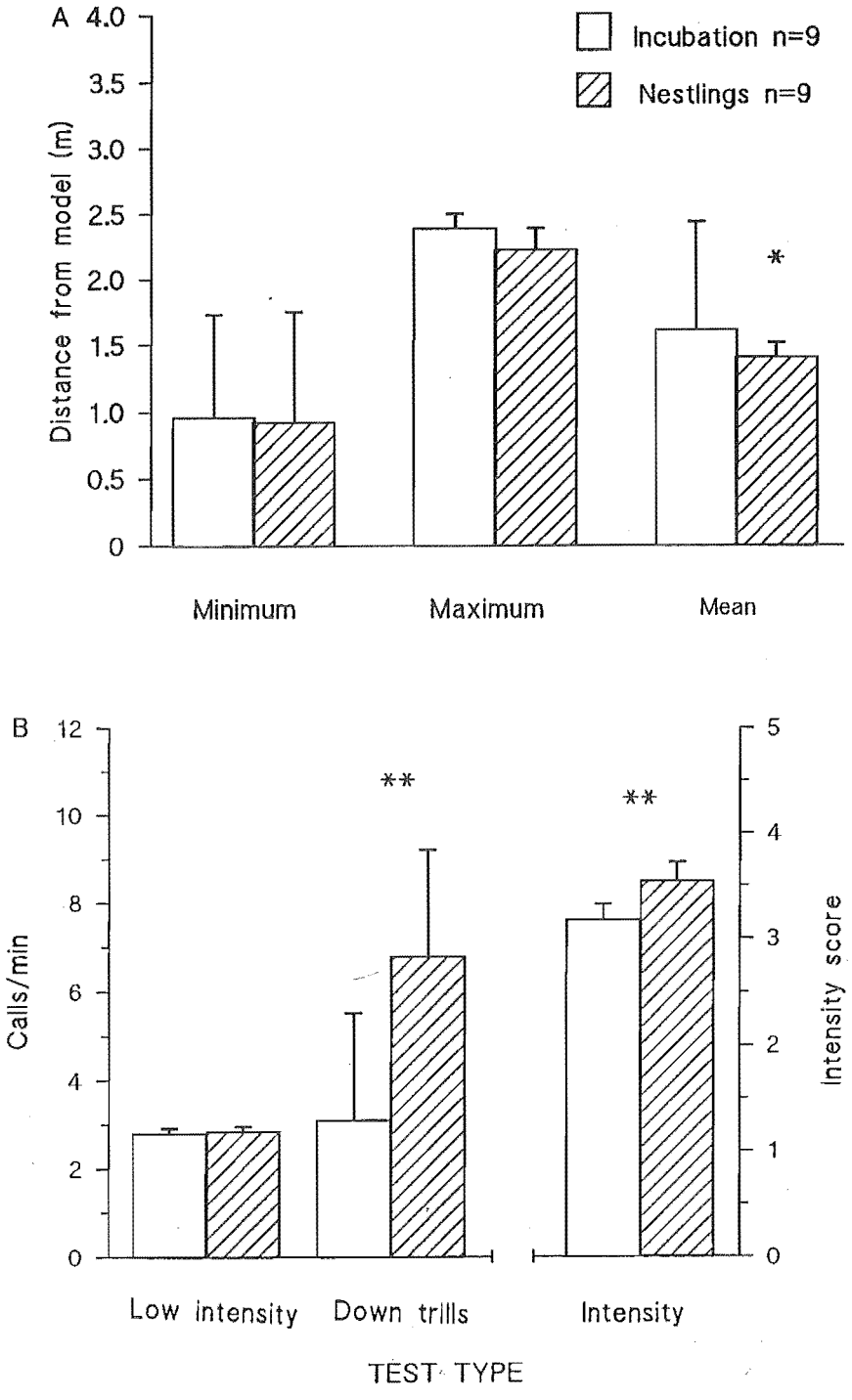

Figure 2.6. Comparison of average nest defence measures for Rifleman nests repeatedly tested at 3 day intervals at the incubation and nestling stages (Wilcoxon sign rank test, mean ± SE, * = $p < 0.05$, ** = $p < 0,01$).

($p<0.05$, 1 tailed, Fig 2.7). Maximum distance, mean distance and the intensity score showed a trend towards increased risk at the nestling stage.

Riflemen also showed significant increases in the level of risk taken to defend nests between the incubation stage and the nestling stage, indicated by reduced minimum distance ($p<0.05$, 1 tailed) and mean distance ($p<0.05$, 1 tailed), and an increased intensity score ($p<0.05$, Fig 2.8). The decrease in minimum distance ($p=0.07$, 1 tailed) and increase in down trills ($p=0.06$, 1 tailed) at the nestling stage approached significance, and all the remaining variables showed a trend towards an increased intensity at the nestling stage.

Nests tested only once compared with nests that were tested repeatedly:

Nests tested only once during incubation were tested on average at day 11.6 for Grey Warblers and day 10.1 for Riflemen. The results from these tests were compared with tests carried out between days 10-12 of incubation at nests that were tested repeatedly. At this stage Grey Warbler parents that had been tested repeatedly had previously experienced an average of 1.7 tests (range 1 to 3) and Rifleman parents an average of 2.8 tests (range 2 to 4).

Grey Warblers and Riflemen showed no significant differences in any behaviour measured between nests tested only once and nests tested repeatedly (Figs. 2.9 & 2.10).

Nests tested only once during the nestling stage were tested on average at day 10.8 for Grey Warblers and day 9.2 for Riflemen. The results from these tests were compared with tests carried out during days 10-12 of the nestling stage for Grey Warbler nests tested repeatedly, and days 7-9 for Riflemen nests tested repeatedly. At this stage parent Grey Warblers had experienced an average of 7.1 tests and parent Riflemen had experienced an average of 8.8 tests.

Grey Warblers at nests tested repeatedly showed a significantly less intense response than nests tested once only, indicated by a greater minimum distance ($p<0.05$), mean distance ($p<0.05$) a smaller intensity score ($p<0.05$), and less alarm calls ($p=0.05$, Fig. 2.11). None of the remaining behaviours were significantly different between the two groups.

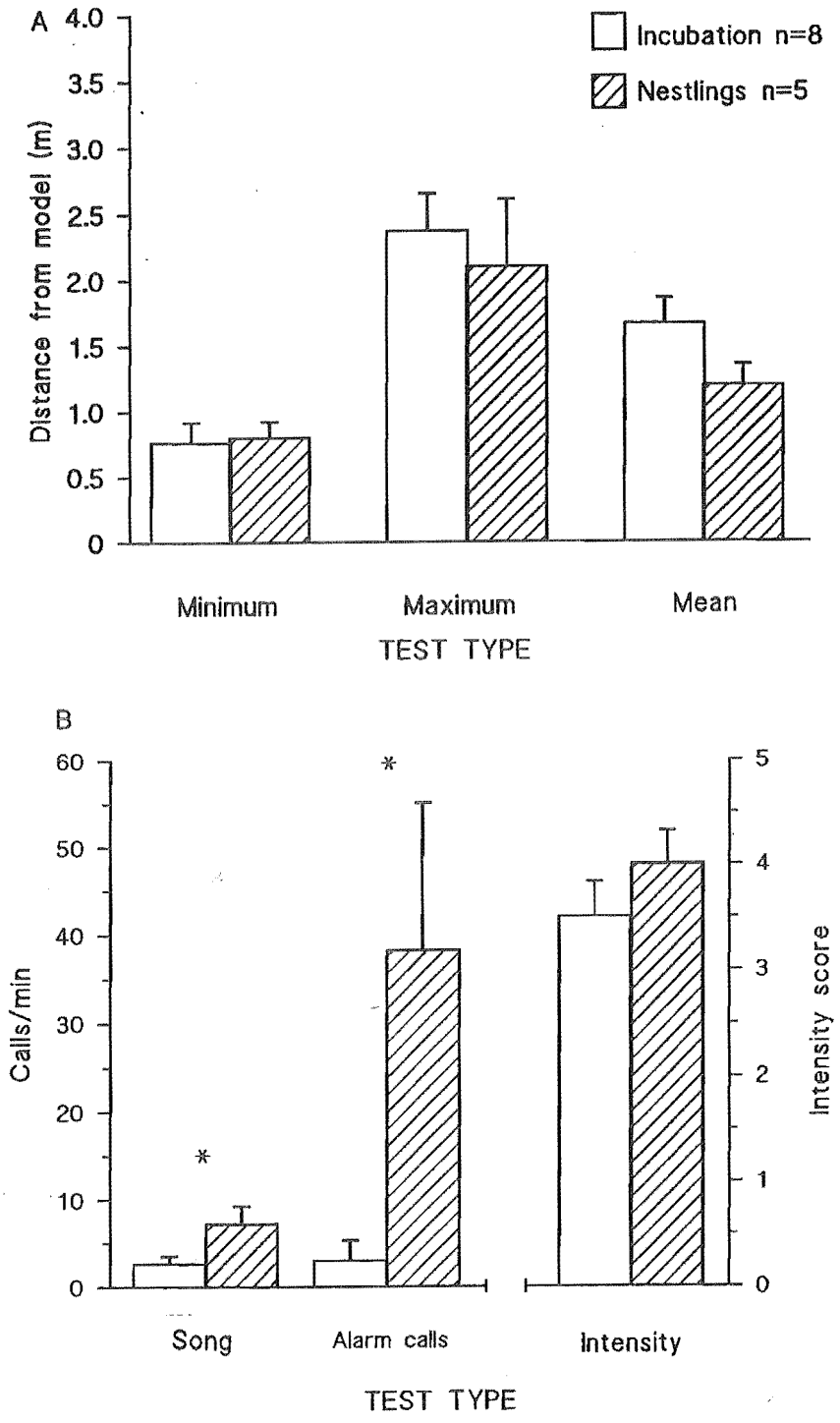

Figure 2.7. Comparison of nest defence measures for Grey Warbler nests tested only once at either the incubation or nestling stage (Mann-Whitney U test, mean ± SE, * = $p < 0.05$).

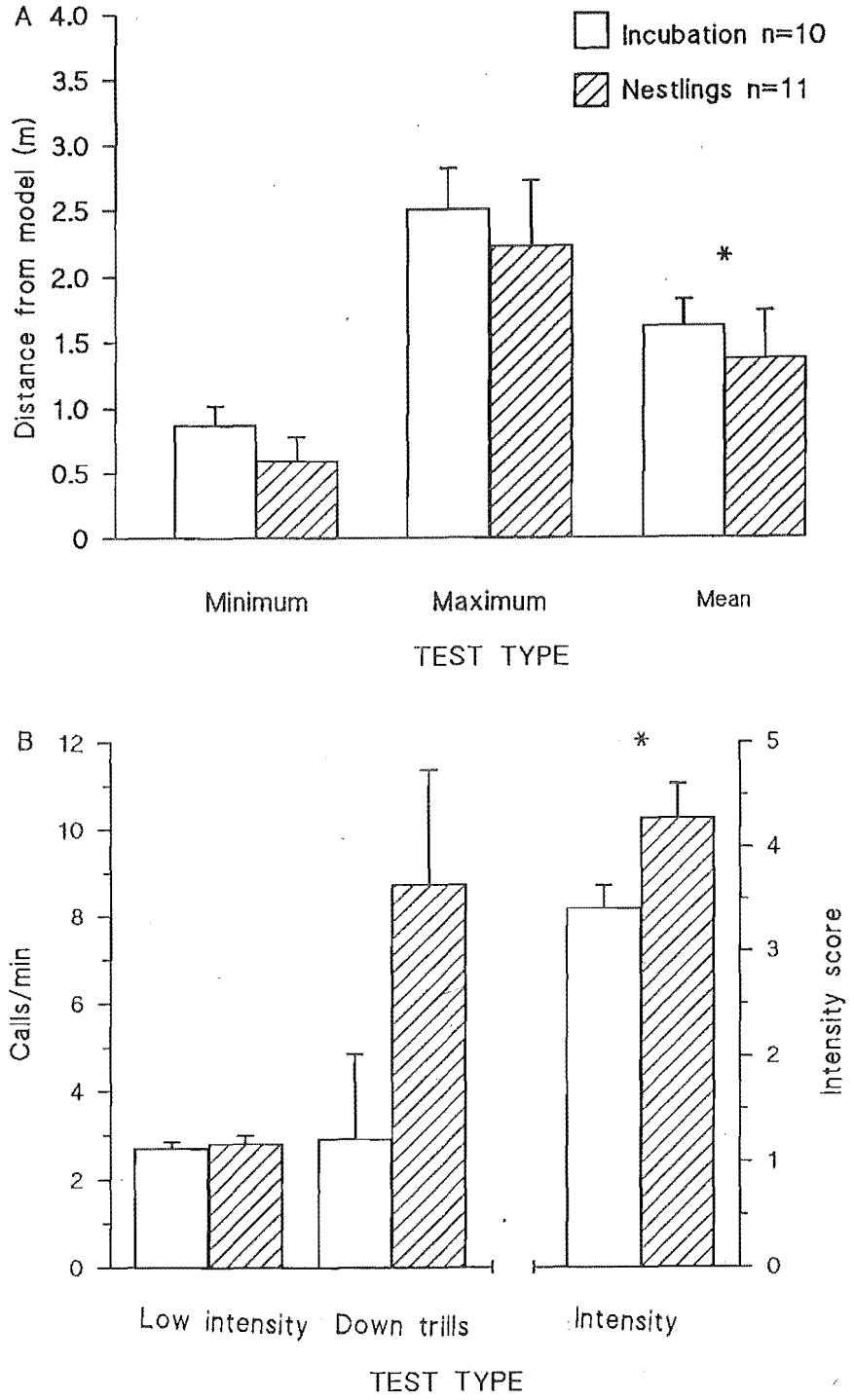

Figure 2.8. Comparison of nest defence measures for Rifleman nests tested once only at either the incubation or nestling stage (Mann-Whitney U test, Mean ± SE, * = $p < 0.05$).

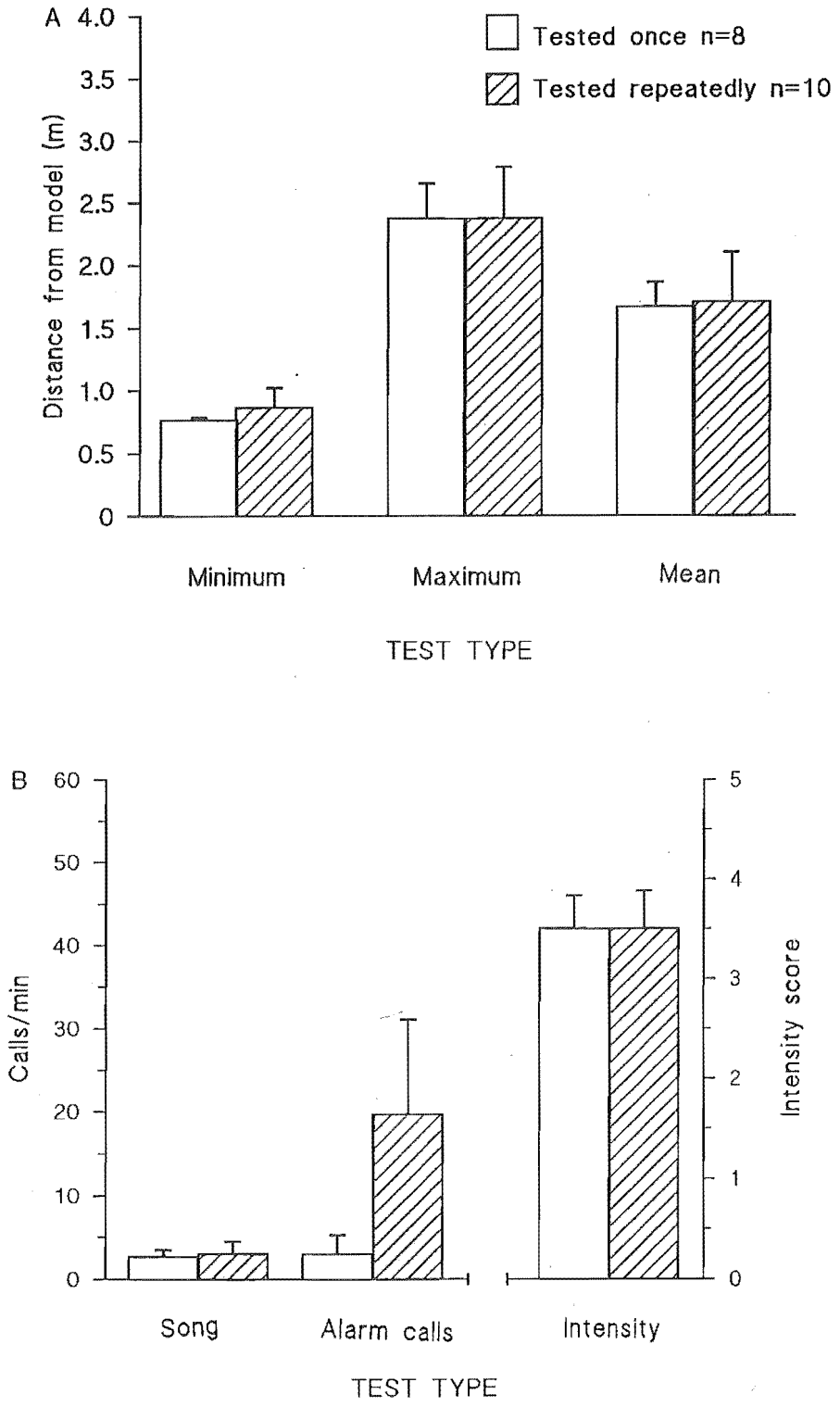

Figure 2.9. Comparison of nest defence measures for Grey Warbler nests tested only once or repeatedly tested at 3 day intervals during incubation (Mann-Whitney U test, mean ± SE, * = $p < 0.05$).

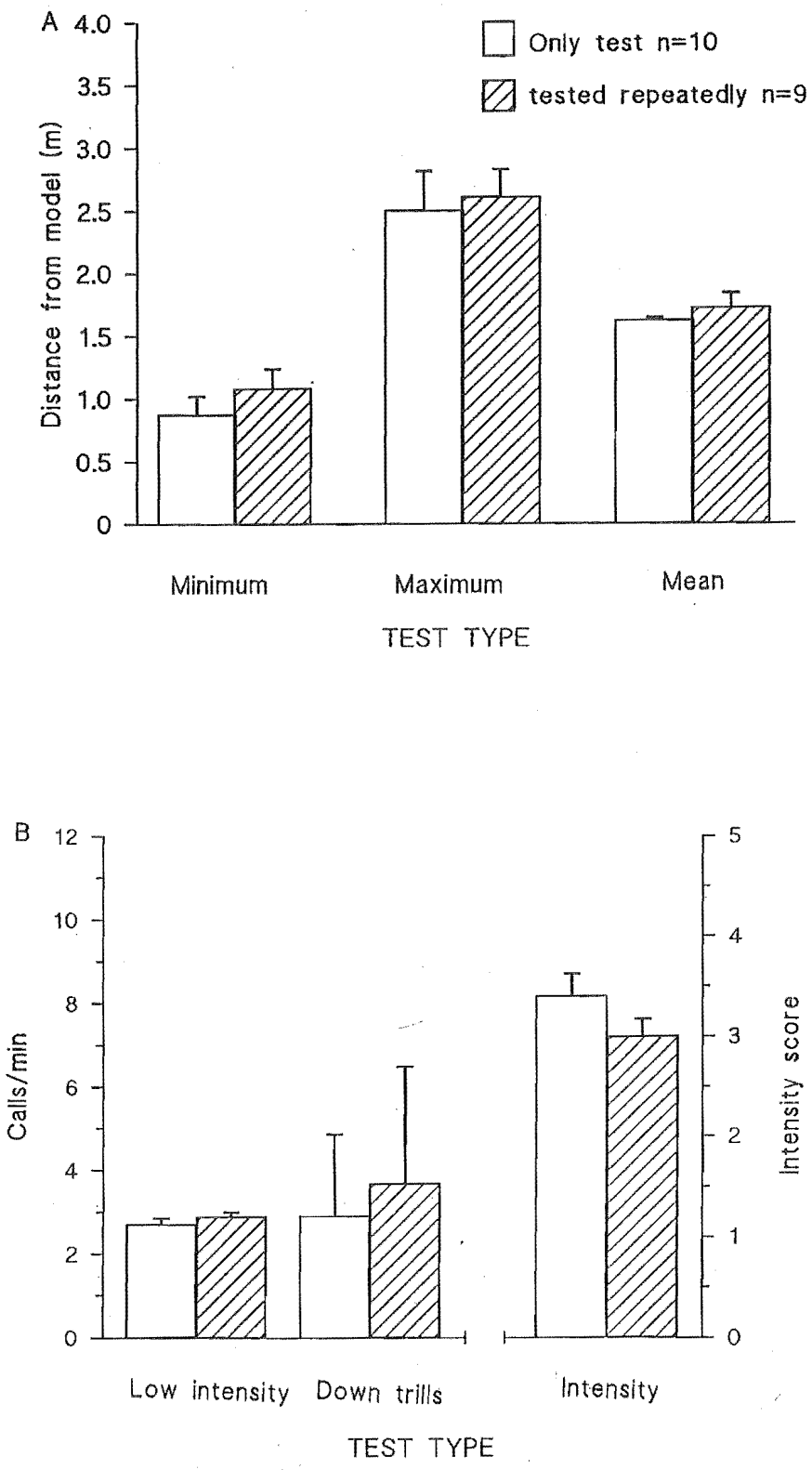

Figure 2.10 Comparison of nest defence measures for Rifleman nests tested only once or repeatedly tested at 3 day intervals during incubation (mann-Whitney U test, mean ± SE, *=$p<0.05$).

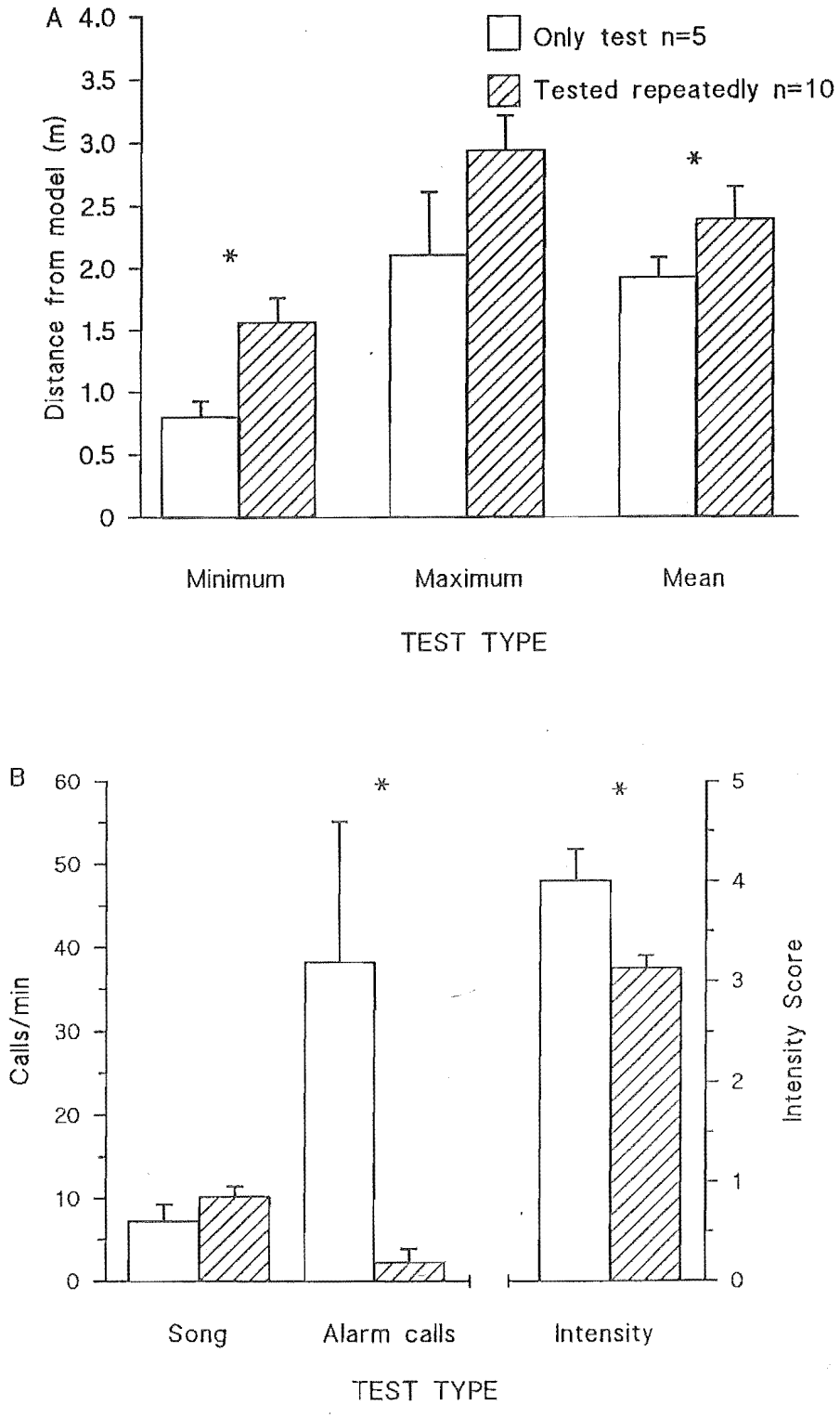

Figure 2.11. Comparison of nest defence measures for Grey Warbler nests tested only once or repeatedly tested at 3 day intervals during the nestling stage (Mann-Whitney U test, mean ± SE, * = $p < 0.05$).

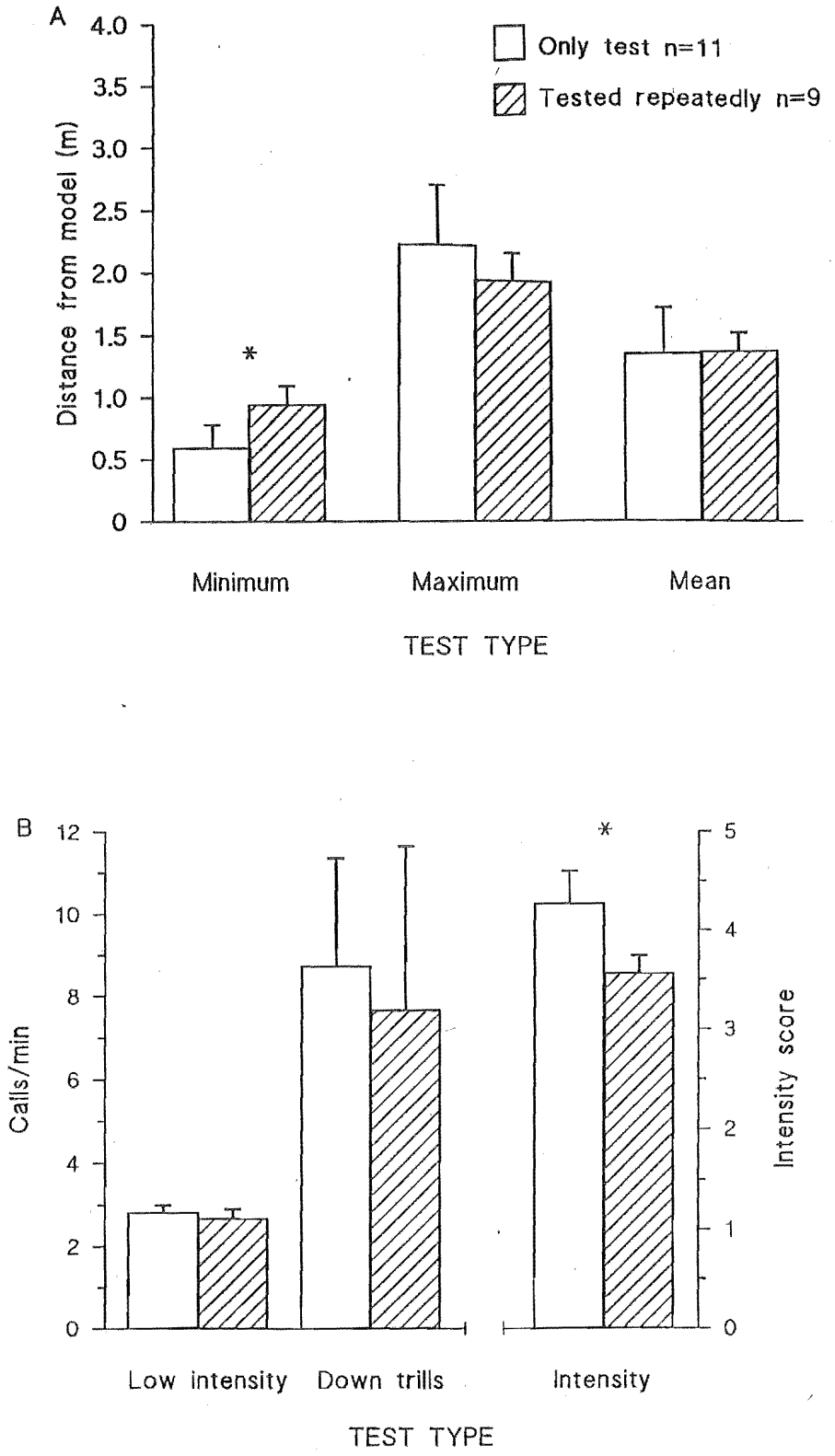

Figure 2.12. Comparison of nest defence measures for Rifleman nests tested only once or repeatedly tested at 3 day intervals during the nestling stage (Mann-Whitney U test, mean ± SE, * = $p < 0.05$).

Riflemen showed a decrease in the intensity score ($p < 0.05$, Fig 2.12). None of the other behaviours were significantly different but minimum distance, mean distance, low intensity calls and down trills showed a trend towards decreased intensity at repeatedly tested nests.

Summary of results

Regression analysis of nest defence behaviours measured at Grey Warbler and Rifleman nests tested repeatedly showed a slight decrease in intensity through the incubation stage and then a rise in intensity after hatching. The increase in nest defence through the nestling stage was stepwise in places for both species. At nests tested repeatedly, the response was greater during the nestling stage than during the incubation stage.

At nests that were tested only once, nest defence response increased between the incubation and nestling stages in both species.

Responses at nests tested repeatedly during incubation did not differ from responses at nests tested only once during incubation. However, by the nestling stage (about 6 tests later) responses at nests that were repeatedly tested were significantly lower than responses at nests tested only once.

DISCUSSION

The results from nests that were tested only once at incubation or the nestling stage clearly showed that the parent birds took a higher risk to defend nestlings than eggs as predicted by both optimality theory and the feedback hypothesis. However, in contrast to predictions of optimality theory and the results of many studies of nest defence, I found that Grey Warbler and Rifleman parents did not gradually increase nest defence intensity as their offspring aged. Results from nests that were tested every three days showed a decrease in the intensity of nest defence through the incubation period followed by an increase into the nestling stage.

A flat or non-significant increase in nest defence through the incubation period

has been found by Curio (1975), Andersson et al. (1980), Grieg-Smith (1980), East (1981), Blancher & Robertson (1982), and Weatherhead (1989). Grey Warbler and Rifleman parents seemed to habituate to the model after it had been presented several times (see discussion of methodology below), because responses at nests tested repeatedly became less intense with repeated presentations. The results of this study would likely show the same trend as the above studies if the effects of habituation could be removed. This result for Grey Warblers would then fit the predictions of the feedback hypothesis (McLean & Rhodes 1991).

Despite the dampening of response attributed to habituation, both Grey Warblers and Riflemen show increased levels of nest defence at the nestling stage. The curve of intensity score of Grey Warbler parents through the nestling stage showed a step function between tests at day 21 (nestlings are two days old) and day 24 (nestlings are five days old). Grey Warbler nestlings first start to call when four days old and by five to six days of age calling is fairly loud (Gill 1983). Calling by the nestlings could increase the stimulus provided to the parents and is correlated with the stepped increase in nest defence at four to five days, lending support to the feedback hypothesis. A second step function can be seen between day 30 (nestlings are 11 days old) and day 33 (nestlings are 14 days old). Between these two days the feathers fully irrupt from the sheaths and the nestlings are developed enough to fledge if threatened further supporting predictions of the feedback hypothesis. Riflemen parents showed an increase in the intensity of their nest defence response immediately after the chicks hatch, but throughout the nestling stage the intensity of the response remained at a fairly constant level. This result does not support either optimality theory or the feedback hypothesis.

Methodology

Knight & Temple (1986a,b) proposed that repeated testing of the same parent birds increased their level of response to a predator at the nest due to positive reinforcement and loss of fear. They further showed that nest defence intensity did not increase in three species of passerines between the incubation and nestling stages when each nest was tested only once. Levels of nest defence responses from

repeatedly tested Grey Warbler and Riflemen parents also differed from response levels from parents tested once only, but not in the way predicted by Knight & Temple (1986a,b). At the incubation stage there was no difference in response between parents that had been tested previously and those that had not been tested before, but at the nestling stage (about 6 tests later) defence reponses by parents tested repeatedly was significantly lower than responses by parents that had never been tested.

This dampening of nest defence response after being repeatedly tested is probably due to habituation of the parents to the model. Habituation to predators in a real situation would seem to be maladaptive. Model predators, although recognised as a threat to the nest by many bird species, cannot provide the same stimulus as a live predator. The continually changing spatial relationship between a predator and the environment is an important component of predator recognition in birds (Shalter 1978b). Some species seem to be more sensitive to the difference between real and model enemies than others. East (1981) found that the European Robin, *Erithacus rubecula*, did not respond to models of a squirrel, jay, or Carrion Crow as they would to a live predator, and Buitron (1983) abandoned experiments with a mounted Horned Owl at Black-billed Magpie, *Pica pica,* nests as they habituated to the model after one exposure. The use of models has been successful with some birds (Biermann & Robertson 1981; Smith et al. 1984; McLean 1987) including Grey Warblers and Riflemen in this study, but it appears that for most species, models should not be repeatedly presented to the same parents.

It is important that a researcher measures behaviours that indicate the intensity of a nest defence response, as some behaviours may not do this. A defence response is made up of a suite of many, often complex behaviours. The parameters used to measure nest defence intensity vary widely between studies. Some of the variation is due to different species using different nest defence behaviours, but most of the variation is due to the behaviours chosen to be measured by researchers (see Table 2.8 for variables measured).

Many studies have used call types and call rates as their only measure of defence intensity or as one of several behaviours measured. Calls are relatively

Table 2.8. Behaviours used to measure nest defence in previous studies.

Behaviour	References
Call types / Call rates	Curio and co-workers; Shalter 1978; Weatherhead 1979, 1982, 1989, 1990; Grieg-Smith 1980; Patterson et al.1980; Knight & Temple 1986; McLean et al 1986; Knight et al. 1987; McLean 1987; Hobson et al. 1988; Briskie & Sealy 1989; Redondo & Caranza 1989; Westneat 1989; Rytkonen et al. 1990.
Loudness of calls	Barash 1975; Grieg-Smith 1980.
Latency of calling	Curio & co-workers*; Redondo & Caranza 1989.
Distance of predator from nest when parent first called	Knight et al 1987.
Minimum distance	Curio & co-workers*; Weatherhead 1979, 1982, 1989; Smith et al. 1984; Knight & Temple 1986; Knight et al. 1987; McLean 1987; Hobson et al. 1988; Redondo & Caranza 1989; Brunton 1990.
Maximum distance	Weatherhead 1982, 1989.
Average distance	Curio & Co-workers*; Hobson et al.1988.
Flushing distance	Knight et al. 1987; Westmoreland 1989.
Number of flights	Smith et al 1984; McLean 1986; McLean 1987.
Subjective categories	Gottfried 1979; Andersson et al. 1980; Blancher & Robertson 1982; Buitron 1983; Bossema & Benus 1988: McLean et al 1986; Chandler & Rose 1988; Brunton 1990; Weatherhead 1990.
Calculated categories	Bierman & Robertson 1981.
Number of swoops and strikes	Lemmetyinen 1971; Knight & Temple 1986 McLean 1986;Knight et al. 1987; McLean 1987; Erwin 1988; Hobson et al. 1988; Wiklund 1990.
Distraction displays	Hobson et al 1988.

*Papers by Curio & co-workers include: Curio 1980; Regelmann & Curio 1983; Curio & Regelmann 1985; Curio et al. 1985; Regelmann & Curio 1986.

easy to record and are a frequent behaviour during nest defence, but may not be the most accurate measure of the risk taken by a bird. Call rates are not as energetically demanding or as risky as other behaviours such as diving on or approaching the predator closely (Knight & Temple 1986b). Alarm calls may be more important for giving information than for directly defending the nest. "Whit" calls in Stonechats, *Saxicola torquata*, are used to quieten chicks or possibly warn a female on the nest of danger (Grieg-Smith 1980). Due to their acoustic properties, some calls may be difficult for predators to locate and so may pose no real risk to the caller (Marler 1955). Calls rates are an important part of nest defence but should not be relied upon to indicate risk taken by a parent bird without the backup of other behaviours.

Proximity to the predator is most likely to accurately reflect the risk taken by a defending bird (Curio et al. 1983; Regelman & Curio 1983; Redondo & Caranza 1989). In previous studies distance of the bird from the predator has been measured in terms of minimum distance, maximum distance, mean distance, latency of attaining minimum distance and flushing distance. I consider minimum distance and mean distance to be the most valuable measures of distance. The minimum distance is the point when the defender is at most risk of being killed or injured by the predator and the mean distance indicates how much time the defender spent close to the predator. Maximum distance was not so important in this study as it was often recorded as the bird was only just aware of the predator and moving towards it.

The number of movements, flights or hops, is a difficult variable to interpret. McLean et al. (1985) and McLean (1987) found that the inclusion of flights did not contribute to the interpretation of the data. Smith et al. (1984) found that the number of flights were useful to indicate differences in intensities of responses. However, a greater number of movements does not necessarily indicate an increase in intensity. The most intense response by a Rifleman in this study was when a male remained 0.5m from the model, without moving, with its wings raised for most of the two minute test period. This response would have scored very low if judged on the number of flights or hops. Flights and hops were recorded in this study but were later rejected due to unreliability in recording them (see Appendix 1).

The intensity of a nest defence response is a complicated mesh of inter-related behaviours. For example, although calling may not be a risky behaviour if performed

several metres away from the predator, it may become a high risk activity if coupled with being in close proximity to the predator. The subjective scale of defence intensity or aggression used in several studies (Andersson et al. 1980; Blancher & Robertson 1982; Buitron 1983; Bossema & Benus 1985; McLean et al. 1986; Chandler & Rose 1988; Brunton 1990; this study) may help to cope with the multi-dimensionality of nest defence responses.

Summary

Although parents at nests that were tested repeatedly showed signs of habituating to the model, patterns of nest defence by Grey Warblers through the breeding season tentatively lend support to the feedback hypothesis. The pattern of nest defence through the breeding season for Riflemen gave partial support to both optimality theory and the feedback hypothesis.

Care must be taken in studies of nest defence where models are repeatedly presented to the same parents as there is a likelihood that habituation to the model will occur. Behaviours used to measure the risk taken by parent birds defending their nests must be chosen carefully as not all behaviours are good indicators of risk.

3. SEX DIFFERENCES IN NEST DEFENCE

INTRODUCTION

The sex of a parent has been found to influence the intensity of a nest defence response in many passerine and non-passerine species. Males tend to defend the nest more vigorously in most species (Curio 1980; East 1981; Wiklund & Stigh 1983; Regelmann & Curio 1985,1986; Andersson & Wiklund 1987; Brietwisch 1988; Weatherhead 1989; Brunton 1990; Sordahl 1990) but females are the primary nest defenders in some other species (Wallin 1987; Hobson et al. 1988; Weatherhead 1989). A few species have shown no differences between the sexes in nest defence (Knight & Temple 1986c; Andersson et al. 1980; Grieg-Smith 1980).

Sexual differences in nest defence behaviour can be expected when there are differences between the sexes in (1) confidence of parenthood, (2) renesting potential, (3) perception of risk, (4) life history characteristics, and (5) the ability to raise offspring unaided (Montgomerie & Weatherhead 1988). None of the above are mutually exclusive, and some factors are likely to drive nest defence intensity in opposite directions to others. Therefore, for any species, each factor must be considered separately.

The confidence of parenthood for a female will almost always be higher than that for a male (Trivers 1972). A male's confidence of parenthood is inversely related to the opportunities for cuckoldry within a population. For example, in the Yellow Warbler, *Dendroica petechia*, males leave most of the nest defence to the female, possibly due to a relatively high frequency of cuckoldry that results in a lowered confidence of paternity (Hobson et al. 1988).

The renesting potential for each sex is affected by biased sex ratios. Great Tits, *Parus major*, have a male-biased sex ratio and the male takes the highest risks in nest defence (Regelmann & Curio 1983; Curio 1980). Males are expected to defend the nest more intensely than females because the male may not be able to replace his mate if she dies.

The risk associated with performing different nest defence behaviours may vary according to sex. In many species the male has brighter plumage than the female,

and therefore the male may face greater danger when approaching a predator than the duller plumaged female (Montgomerie & Weatherhead 1988). Species that are sexually dimorphic in size may also show sexual differences in nest defence behaviour. The smaller sex may be the primary nest defender due to greater manoeuvrability as suggested in male Snowy Owls, *Nyctea scandiaca*, (Wiklund & Stigh 1983) and Rough-legged Buzzards, *Buteo lagopus*, (Andersson & Wiklund 1987). Alternatively, the larger sex may defend more vigorously due to greater strength as in female Tawny Owls, *Strix aluco*, (Wallin 1987). Nest defence by females may be more risky in the period after they have finished laying their eggs. Species that lay a large percentage of their body weight may be physically weakened so defence of the nest becomes more risky. The condition of the female has been shown to affect nest defence in the Tawny Owl (Wallin 1987).

Life history characteristics such as a differing mortality rate between the sexes may influence nest defence behaviour. If one sex suffers a higher mortality rate, then its chances of reproducing the next season are less than that of its mate and so a more intense defence response can be expected.

The risk taken by a parent to defend its offspring may also be affected by the ability of the parent to raise the offspring without its mate. In many species, the male is unable to raise a brood on his own until the nestlings no longer require brooding by the female. Since males lose the clutch if the female dies, then males are expected to take greater risks than their mate.

Whether the presence of a mate affects a bird's nest defence response has not been fully examined. Regelmann & Curio (1986) found that a male Great Tit, *Parus major*, in the presence of its mate will approach a predator more closely than when the female is absent. They explained this as (1) the male placing himself between the predator and his mate to protect the mate, or (2) the male persuading the female that he is a quality mate.

Several studies have found that members of a pair co-operate in defence (Bossema & Benus 1985; Regelmann & Curio 1985; Buitron 1983). In the Carrion Crow, *Corvus corone*, members of a pair cooperate by responding simultaneously and mutual encouragement (Bossema & Benus 1985). Without the cooperation and encouragement of a mate, how would a bird alter its defence response? I suggest that there are three possible ways that a bird would react in defence of its

nest without its mate present:
(1) defence intensity may be increased to compensate for being the only defender, (2) nest defence intensity may decrease as a single bird may be more at risk performing the same behaviours than when there are at least two birds responding, or males do not need to impress or protect a mate, and (3) defence intensity would remain the same if the level of response was based on the risk to the nest posed by the predator, independent of a mate's presence.

Members of a pair may not only work together in nest defence but may be matched with respect to the intensity of their responses. That is, a male that strongly defends its nest will have a mate that also strongly defends the nest. Brietwisch (1985) found Mocking bird, *Mimus polyglottos*, pairs had highly correlated levels of defence. He proposed three possible hypotheses as to why Mockingbird mates responded with the same intensity: (1) Mate choice by both sexes may be linked to defence intensities, (2) Females may be matching their level of response to their mate's response, and (3) environmental characteristics around the nest may affect defence responses. Environmental characteristics were rejected as a possibility in Mockingbirds.

In this section of my study of nest defence by Grey Warblers and Riflemen I investigate the differences in nest defence between the sexes for each species. Grey Warblers and Riflemen are both small, insectivorous, double brooded passerines, but they differ in some aspects of their social organisation which may affect the nest defence responses of each sex.

Grey Warblers and Riflemen are monogamous throughout the year. Confidence of parenthood in both species is probably fairly high as male Grey Warblers guard their mates over the fertile period (Gill 1980; Cameron 1990), and Rifleman pairs spend most of their time together (Sherley 1985). A high level of parental care by the male Rifleman also suggests a high confidence of parenthood (Sherley 1985). The population ratio is probably slightly biased towards males for both species (Gill 1980; Sherley 1985). Grey Warblers and Riflemen differ in the amount of cooperation within a pair to establish a clutch. Female Grey Warblers build the nest on their own, lay a clutch that is approximately 92% of their body weight and incubate the eggs on their own (Gill 1980). For Riflemen, both birds build the nest, the female lays a clutch approximately 85-100% of her body weight,

is fed by the male while laying, and both sexes share incubation (Sherley 1985). Therefore, a female Grey Warbler seems to invest more to establish a successful nest than a female Rifleman. Mortality rates are similar for both sexes of both species. Male Grey Warblers cannot raise a brood on their own at least until the nestlings no longer require brooding by the female. Male Riflemen have a brood patch and incubate eggs and brood chicks, so a male Rifleman could potentially raise a brood, of a younger age, on his own than a male Grey Warbler. Therefore, in Grey Warblers, males should defend nests more intensely than females because if a male loses his mate the nest will fail whereas, a male Rifleman could potentially raise the brood himself. Predicting nest defence differences between the sexes based on the above information I would expect male Grey Warblers to defend their nest more intensely than the female, but male and female Riflemen to defend their nests fairly evenly.

I asked the following questions:

1. Do females and males differ in nest defence behaviours in Grey Warblers and Riflemen?
2. Are nest defence attendance patterns for females and males the same in Grey Warblers and Riflemen?
3. Does the absence of a mate affect the nest defence intensity of the responding bird?
4. Is the defence intensity of mates correlated?

METHODS

Data for this section were taken from experiments reported in Chapter 2 and performed during the 1989-90 and 1990-91 field seasons at Kowhai Bush, Kaikoura. Grey Warbler and Rifleman nests were tested with the Litte Owl, *Athene noctua*, once only during the incubation or nestling stages (groups 1 and 2), or repeatedly tested every three days throughout the incubation and the nestling stages (group 3). Data from all three groups were used to investigate how females and males defended their nests with and without their mate present and to test for sexual differences in nest defence behaviours.

Nest defence responses of female and male Grey Warblers and Riflemen were measured by placing the model between 1 and 2 metres from nests. Once one or both parents had seen the model their behaviour was recorded for a period of two minutes. The behaviours recorded and analysed in this section are the same as those used in Chapter 2; that is the maximum distance from the model, minimum distance from the model, mean distance from the model, intensity score, and the number and type of vocalisations (see Chapter 2 Methods for a full explanation).

Female and male defence responses for both species were computed using data taken from the nests tested once only during the incubation and nestling stage and the first tests at nests that were tested repeatedly. The proportion of incubation to nestling tests was the same for female and male categories. The percentage of tests attended by each sex for both species was calculated using the 10 Grey Warbler and 9 Rifleman nests that were tested repeatedly.

Nest defence behaviours of female and male when their mates were also defending the nest were compared with nest defence behaviours when their mate was not present for both species. Data were taken from nests tested only once and the first tests from nests tested repeatedly.

An intra-pair comparison of defence was made by performing a correlation analysis using scores from each member of a pair from tests where both parents responded. Nests used in this analysis were from nests tested once only and the first test where both parents responded at nests tested repeatedly.

Data were analysed using Mann-Whitney U tests or correlation analysis. All statistical tests are 2 tailed.

RESULTS

Female and male Grey Warblers did not differ in intensity for any of the behaviours measured except for song; males sang significantly more than females (Table 3.1; Mann-Whitney U test, $p<0.001$). There was a non-significant tendancy for males to alarm call more than females (Mann-Whitney U test, $p=0.08$).

Female and male Riflemen did not differ in any of the behaviours measured

Table 3.1. Differences in male and female nest defence responses in the Grey Warbler and the Rifleman (Mann-Whitney U Test; mean ± SE, NS = p>0.1).

Grey Warbler Behaviour	Female (n=25)	Male (n=26)	p
Maximum distance (m)	2.59 ± 1.16	2.54 ± 1.00	NS
Minimum distance (m)	1.03 ± 0.77	1.00 ± 0.60	NS
Mean distance (m)	1.88 ± 0.89	1.75 ± 0.83	NS
Intensity	3.48 ± 1.03	3.48 ± 0.96	NS
Song (no./min.)	0.17 ± 0.65	4.92 ± 3.59	<0.0001
Alarm calls (no./min.)	8.96 ± 21.9	12.04 ± 21.8	0.08
Rifleman Behaviour	**Female (n=23)**	**Male (n=25)**	**p**
Maximum distance (m)	2.56 ± 1.18	2.67 ± 1.39	NS
Minimum distance (m)	0.96 ± 0.56	0.91 ± 0.62	NS
Mean distance (m)	1.93 ± 1.06	1.69 ± 0.86	NS
Intensity	3.24 ± 0.19	3.39 ± 0.19	NS
Low intensity calls	2.76 ± 0.60	2.78 ± 0.51	NS
Down trills (no./min.)	2.48 ± 6.62	4.15 ± 10.3	NS

(Table 3.2).

Grey Warblers (female or male) did not differ in the intensity of any behaviour measured when defending their nests by themselves or with their mate (Table 3.2). This was also the case for Riflemen (Table 3.3).

At Grey Warbler nests that were tested repeatedly (n=10), females on their own attended 23% of tests and attended 83% of tests overall, and males on their own attended 17% of tests and attended 77% of tests overall. Both parents were present at 60% of all tests. There was no significant difference in attendance rates of females and males either when attending on their own (Mann-Whitney U test, $p>0.2$) or in their overall attendance (Mann-Whitney U test, $p>0.3$). At Rifleman nests tested repeatedly (n=9) females on their own attended 15% of tests and attended 74% of tests overall, and males on their own attended 26% of tests and attended 85% of tests overall. Both parents were present at 59% of all tests. There was no difference in attendance rate between the sexes where only one parent attended (Mann-Whitney U test, $p>0.2$) or in overall attendance rate (Mann-Whitney U test, $p>0.4$).

There was no difference between Grey Warblers and Riflemen in the proportion of nests attended by both parents (Mann-Whitney U test, $p>0.9$).

Data from the first tests where both parents attended from Rifleman and Grey Warbler nests were used in a correlation analysis to determine if pairs are matched for nest defence intensities. There was a significant correlation between members of Rifleman pairs (n=17) for intensity score ($r=0.8279$, $p<0.001$), maximum distance ($r=0.6207$, $p<0.01$), minimum distance ($r=0.5112$, $p<0.05$), and mean distance ($r=0.6354$, $p<0.01$) (Fig 3.1). Females that responded intensely were mated to males that also responded intensely. The responses of Grey Warbler pairs (n=14) were positively but not significantly correlated with, intensity score ($r=0.4226$, $p>0.1$), maximum distance ($r=0.1371$, $p>0.1$), minimum distance ($r=0.4170$, $p>0.1$) and mean distance ($r=0.4121$, $p>0.1$) (Fig 3.2). Female and male Grey Warblers did not seem to defend their nests with similar intensities.

Table 3.2. Differences in nest defence responses when mate present and mate absent in Grey Warblers (Mann-Whitney U Test; mean ± SE, NS = p>0.1).

Female Behaviour	Mate present (n=14)	Mate absent (n=11)	p
Maximum distance (m)	2.46 ± 0.29	2.78 ± 0.43	NS
Minimum diatance (m)	1.07 ± 0.25	0.96 ± 0.62	NS
Mean distance (m)	1.78 ± 0.24	2.03 ± 0.30	NS
Intensity	3.14 ± 0.29	3.22 ± 0.32	NS
Song (no./min.)	0.21 ± 0.21	0.11 ± 0.11	NS
Alarm calls (no./min.)	7.79 ± 4.21	10.11 ± 10.11	NS
Male Behaviour	**Mate present (n=14)**	**Mate absent (n=9)**	**p**
Maximum distance (m)	2.43 ± 0.21	2.78 ± 0.37	NS
Minimum distance (m)	0.92 ± 0.13	1.09 ± 0.22	NS
Mean distance (m)	1.59 ± 0.12	1.95 ± 0.34	NS
Intensity	3.57 ± 0.23	3.36 ± 0.34	NS
Song (no./min.)	6.00 ± 0.94	3.55 ± 1.01	0.09
Alarm calls (no./min.)	9.64 ± 3.25	15.09 ± 9.18	NS

Table 3.3. Difference in nest defence when mate present and mate absent in Riflemen (Mann-Whitney U Test; mean ± SE, NS = p>0.1).

Female Behaviour	Mate present (n=12)	Mate absent (n=12)	p
Maximum distance (m)	2.88 ± 0.38	2.27 ± 0.28	NS
Minimum distance (m)	1.14 ± 0.18	0.78 ± 0.12	NS
Mean distance (m)	2.12 ± 0.27	1.51 ± 0.19	0.08
Intensity	2.92 ± 0.26	3.54 ± 0.27	NS
Low intensity calls	2.67 ± 0.25	2.85 ± 0.10	NS
Down trills (no./min.)	1.33 ± 1.09	3.54 ± 2.36	NS
Male Behaviour	**Mate present (n=12)**	**Mate absent (n=12)**	**p**
Maximum distance (m)	3.25 ± 0.51	2.18 ± 0.18	NS
Minimum disatnce (m)	1.04 ± 0.96	0.80 ± 0.16	NS
Mean distance (m)	1.99 ± 0.31	1.43 ± 0.14	NS
Intensity	3.25 ± 0.28	3.50 ± 0.27	NS
Low intensity calls	2.83 ± 0.17	2.71 ± 0.13	NS
Down trills (no./min.)	2.41 ± 1.10	5.64 ± 3.58	NS

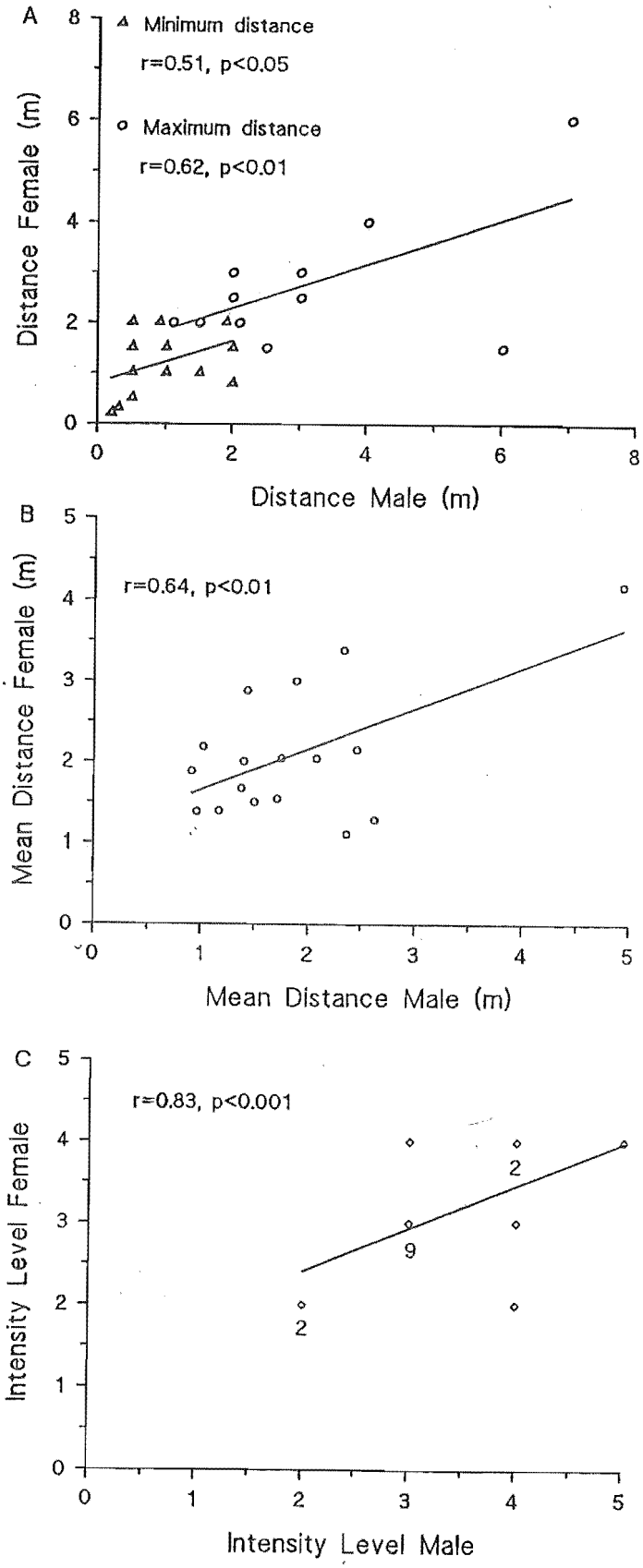

Figure 3.1. Correlation of nest defence measures within Rifleman pairs (n=17). A) Minimum and maximum distances, open symbols represent 1 sample whereas closed symbols represent 2 or more samples. B) Mean distance. C) Intensity score, numbers indicate sample sizes.

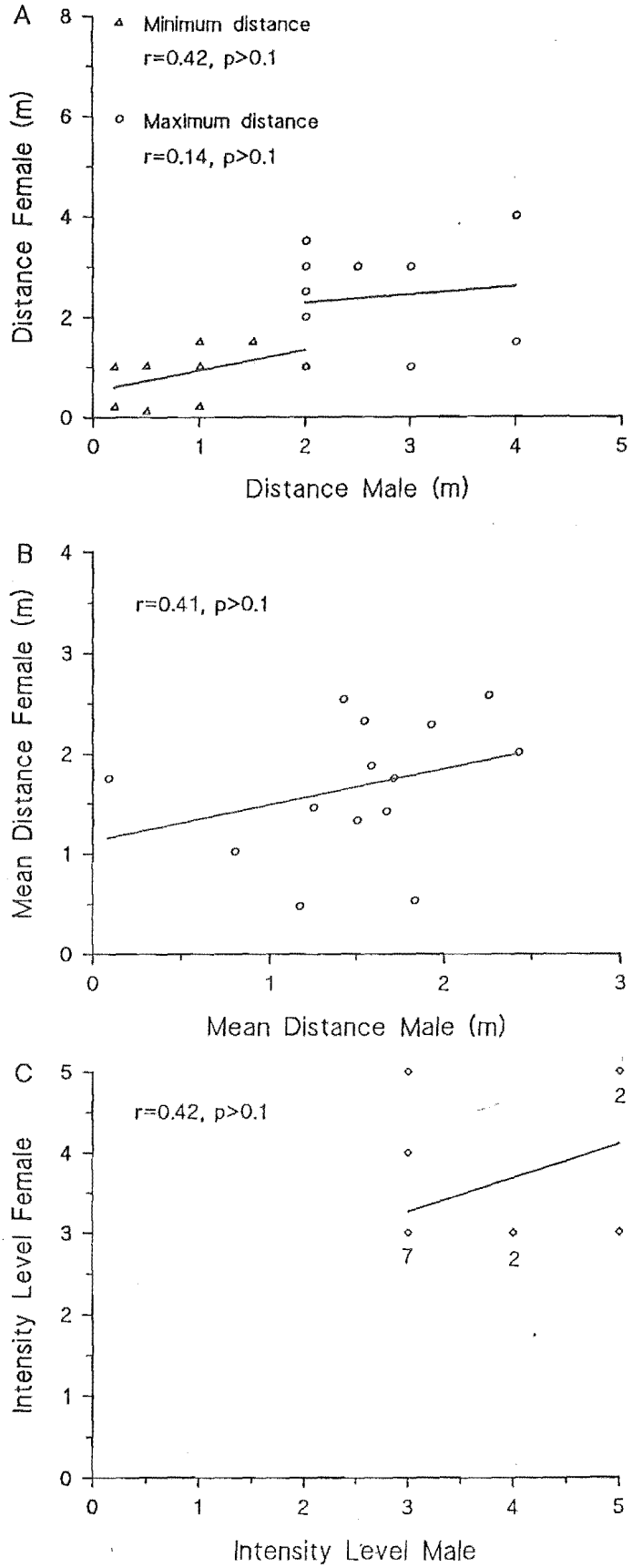

Figure 3.2. Correlation of nest defence measures within Grey Warbler pairs (n=14) A) Minimum and maximum distances, open symbols represent 1 sample whereas closed symbols represent 2 or more samples. B) Mean distance. C) Intensity score, number indicate sample sizes.

DISCUSSION

Female and male Grey Warblers did not differ in defence intensity for any of the behaviours measured, including the proportion of tests attended, except that males sang more than females. Calling while defending a nest from an owl places a bird more at risk than if it is silent, as owls have been shown to orientate towards the direction of calls (Shalter & Schleidt 1977; Shalter 1978c). As males called more and all other behaviours measured did not differ between the sexes, males seemed to be taking a slightly greater risk than females. This finding is consistent with the predictions based on the five factors listed by Montgomerie & Weatherhead (1988) for sexual differences in nest defence, but as all of the other behaviours recorded show no difference between the sexes this result must be regarded with caution. Males were expected to take higher risks due to a male biased sex ratio, and the inability of males to raise a brood on their own until the chicks no longer required brooding, but this was not confirmed by the results. A factor that might have pushed the higher risk-taking towards the female was the chance of the male being cuckolded, but this is likely to be small due to mate guarding (Cameron 1990; Gill 1980).

Female and male Riflemen did not differ in the risk taken to defend the nest in any of the behaviours measured or the proportion of tests attended. Nest defence in this species is a shared task as are all of the other parental care tasks. This is consistent with my prediction that nest defence would be similar between the sexes in Riflemen using Montgomerie & Weatherhead's (1988) criteria.

The proportion of tests attended by both sexes was the same for both species. Although Grey Warblers showed greater sexual division of labour in most areas of parental care compared to Riflemen, this difference did not seem to be as exaggerated in nest defence.

Nest defence intensity of females and males is not dependent on the presence of a mate in Grey Warblers and Riflemen. I found no difference in any of the measured behaviours of birds defending their nest with their mate, compared with those birds defending the nest alone. This finding rejects the hypotheses that in Grey Warblers or Riflemen intensity may fall due to a lack of encouragement from a mate or that intensity may rise as the bird either tries to compensate for being the only defender, to impress a mate, or to protect a mate.

Rifleman pairs appear to be matched with respect to the intensity of a nest defence response, whereas Grey Warbler pairs were less so. Breitwisch (1985) found that Mockingbird, *Mimus polyglottos*, pairs had highly correlated levels of defence. He proposed mate choice, females matching their mates level of defence, or characteristics of the environment around the nest as explanations of this trend.

In Riflemen it is possible that mate choice may involve nest defence intensity. Female Red-winged Blackbirds, *Agelaius phoniceus*, could potentially choose their mates for their nest defence qualities (Weatherhead 1990), as epaulette size in males correlates with nest defence ability (Ekert & Weatherhead 1987). Male Riflemen have no obvious characteristic such as epaulettes which might signal their nest defence capabilities to females. Territorial disputes are rare in Riflemen (Cameron 1990; pers. obs.) and so it is unlikely that females could use territorial defence to evaluate a potential mate's nest defence abilities.

Riflemen may match their own nest defence intensity to that of their mate. I suggest that in Riflemen it is just as likely that the male adjusts his level of defence to the female, or that both sexes may tend to alter their defence intensity towards each other.

Environmental characteristics around the nest have been found to affect nest defence responses in birds (Regelmann & Curio 1983; Curio et al. 1985; McLean et al. 1986). Brietwisch (1985) rejected environmental factors as a possible cause of correlated levels of defence within Mockingbird pairs and it is also unlikely to be a factor in this study. All Riflemen nested in the nestboxes provided in Habitat 1 (see Chapter 1, study site) and all Grey Warblers nested in Kanuka trees in relatively similar situations so there were no obvious differences in environmental characteristics between nest sites.

It appears that the confidence of parenthood, renesting potential, perception of risk, life history characteristics and the ability to raise a brood unaided, (Montgomerie & Weatherhead 1988) can be useful for interpereting nest defence responses of the sexes in some species (eg. Riflemen) but not in others (eg. Grey Warblers). As expected benefits are equal for females and males at any stage of the nesting cycle for Grey Warblers and Riflemen, it is perhaps not surprising that defence levels are similar between the sexes.

4. THE EFFECT OF PREDATOR TYPE ON NEST DEFENCE BY RIFLEMEN.

INTRODUCTION

Parent birds have been shown to be able to recognise different predator types and adjust their nest defence response accordingly. It is not uncommon for a bird species to differentiate between terrestrial and avian nest predators (Gottfried 1979; Patterson et al. 1980; East 1981; Gottfried et al. 1985; Brunton 1990). Black-billed Magpies, *Pica pica*, are able to differentiate between different species of raptors (Buitron 1983), and Great Tits, *Parus major*, exhibit different defence responses towards two species of owl (Curio et al. 1983).

Differences in defence responses can involve the use of different calling patterns for different predator types in some species. The Robin, *Erithacus rubecula*, responds to avian nest predators mainly with "seep" alarms, whereas the "tic" alarm is mostly used for squirrels and other terrestrial predators (East 1981). Gottfried et al. (1985) found that American Robins, *Turdus migratorius*, were more likely to respond to a model Blue Jay, *Cyanocitta cristata*, with "chirps" rather than "chucks", whereas a rubber snake elicited similar numbers of "chirps" and "chucks". Vocalisations of the parents that attacked the Blue Jay model contained significantly more "chirps" than those given by parents that did not attack. These results suggest that vocalisations may signal an individual's intention to attack. Alternatively, especially in colonial nesting species, different calls may indicate the nature of the predator to other conspecifics, allowing them to respond appropriately.

The intensity of a nest defence response may also vary with predator type. Redondo's (1989) model of avian nest defence predicts that nest defence intensity should be lower if the risk to the parent from the predator is high.

The risk to a parent from a predator is related to the mobility and armoury of the predator (Montgomerie & Weatherhead 1988). When the nest is threatened by a dangerous predator, parent birds often respond at greater distances (Kruuk 1964) or perform less risky behaviours (Curio 1975), than for a less dangerous

enemy. For example, Lapwings, *Vanellus vanellus*, strike Carrion Crows, *Corvus corone*, which pose little threat to the defending parent, but Red Foxes, *Vulpes vulpes*, are never physically attacked and are circled overhead (Elliot 1985). Blue Herons, *Florida caerulea*, defend their nests against small predators and conspecifics but do not defend their nests against large mammals (Werschkul 1979).

I tested nest defence responses of incubating Riflemen to models of a Little Owl, *Athene noctua*, a Ship Rat, *Rattus rattus*, and a Song Thrush, *Turdus philomelos clarkei*. Little Owls prey on small passerines, particularly during the breeding season (Rule 1977) and are a threat to parent Riflemen because they are highly mobile, with a strong bill and claws. Ship Rats do not have such armourment and do not pose a threat to the parent birds. Song Thrushes are not a predator and this model acted as a stimulus control.

From Redondo's (1989) prediction that nest defence intensity should be lower when parents are faced with a more dangerous predator, I expected Riflemen to defend their nests with more intensity against the rat than the Owl, as the rat poses less risk to the parents. The thrush should not be responded to as strongly as either the owl or the rat, as the thrush is not a threat to the nest contents.

METHODS

Twelve Riflemen nests at Kowhai Bush, Kaikoura were used for this section of the study. Each nest was presented with a model of a Little Owl, a Ship Rat and a Song Thrush.

Nests were first tested between 10 and 13 days ($\bar{x}=11.5$) into the incubation period. All three models (realistic taxidermic mounts) were of similar colouration and size (Fig 4.1). The three models were presented in varying order to each nest on consecutive days. The six possible combinations were randomly assigned to nests with each combination used twice, as there were 12 nests. The procedure for all three models was the same as the presentation of the Little Owl in Chapters 2 and 3. Each model was positioned between 1 and 2m opposite and level with the nest box entrance while one parent was incubating. The parent on the nest was unaware of the model's presence prior to leaving the nest.

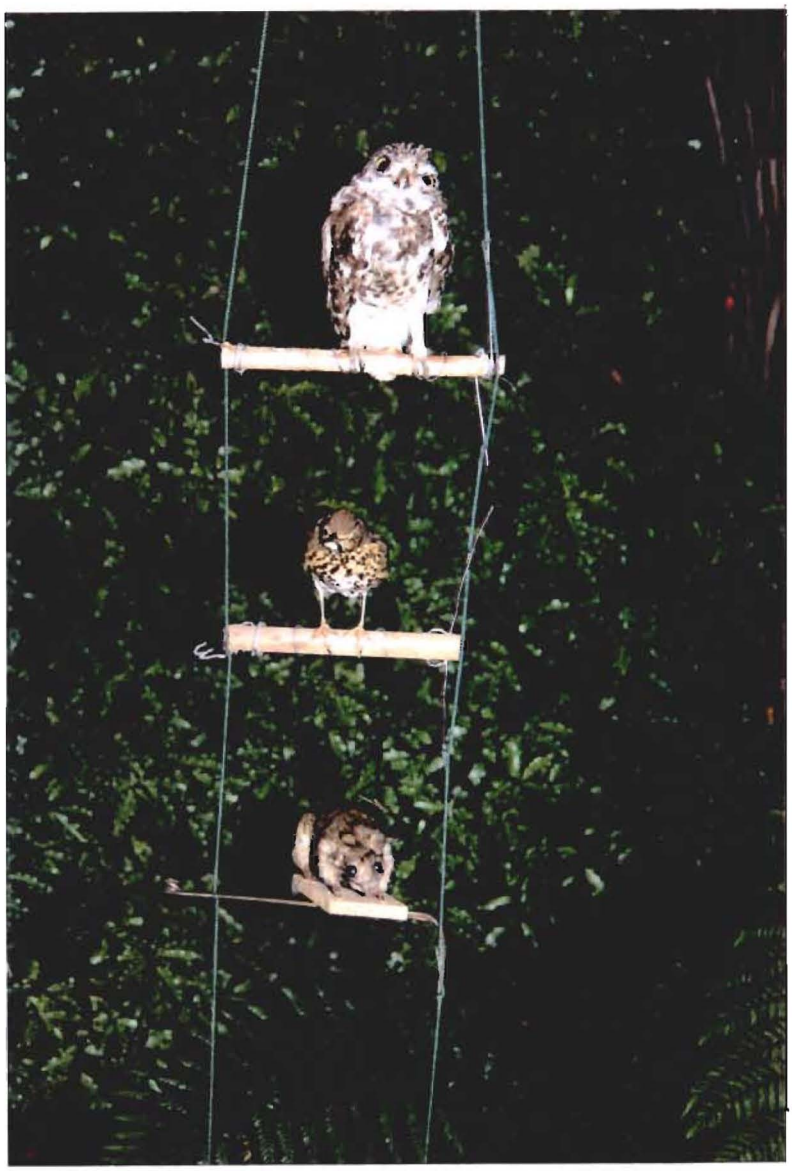

Figure 4.1. Models of the Little Owl, *Athene noctua*, the Song Thrush, *Turdus philomelos clarkei*, and the Ship Rat, *Rattus rattus*.

Once one or both parents had returned to the nest and seen the model, their behaviour was recorded for a two minute period. Behaviours recorded were the same as those recorded for Riflemen in Chapter 2; that is, the minimum distance, maximum distance, mean distance, intensity score, number of low intensity calls and number of down trills. After the two minute test period the model was removed and the birds were watched until incubation was resumed. The time taken from the removal of the model until one of the parents resumed incubation was noted.

All model tests for this section were carried out between 0800 and 1200 hours. If both parents were present at a test, both their responses were recorded. However,
only the response of the bird with the most intense reponse was used in the analysis (regardless of sex). Differences in nest defence responses between the three models were analysed using a Friedman 2 way nonparametric ANOVA.

RESULTS

Order of presentation had no effect on any of the behaviours measured (Friedman's ANOVA, $p > 0.3$ for all values of X^2).

A significant difference in response intensity was found between the three models for intensity score (Friedman's $X^2 = 6.64$, $p < 0.05$), low intensity calls ($X^2 = 12.56$, $p = 0.001$) and the time taken to resume incubation ($X^2 = 6.50$, $p < 0.05$; Fig 4.2a, b & c). The pattern for intensity in these variables was owl > rat > thrush.

Only one parent used down trill alarm calls during the model tests. For this bird the owl elicited more down trills (12) than the rat (2) or the thrush (2).

The three distance measures were not significantly different between the three models; minimum distance (Friedman's $X^2 = 2.11$, $p > 0.1$), maximum distance ($X^2 = 5.21$, $p = 0.07$), and mean distance ($X^2 = 3.51$, $p > 0.1$; Fig 4.2d). The trend for approach distance was owl < rat < thrush.

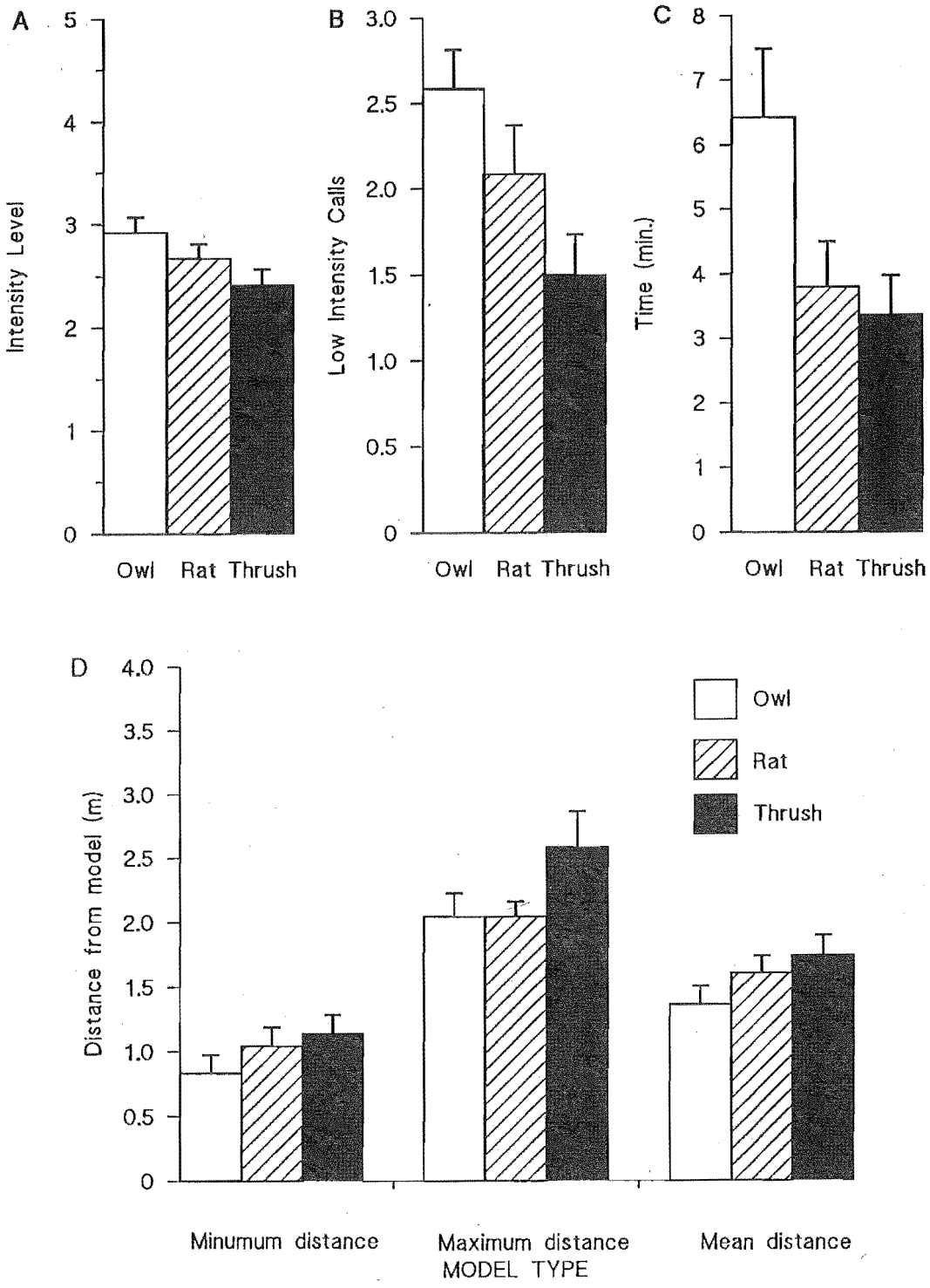

Figure 4.2. Nest defence responses of Riflemen to realistic models of the Little Owl, Ship Rat and Song Thrush. (Friedman 2 way ANOVA, mean ± SE, * = $p < 0.05$, ** = $p < 0.01$).

DISCUSSION

Previous studies have found that predators that were a greater risk to parent birds were responded to with a lower level of nest defence response (Kruuk 1964; Graul 1975; Werschkul 1979; Elliot 1985). The same trend was not found for Riflemen in this study. My results do not support the prediction that nest defence responses will be lower if the risk to a parent from a predator is high. The Little Owl poses a greater threat to an adult Rifleman than a Ship Rat, and yet the owl was approached more closely, elicited more calls and was generally responded to more intensely than the rat. Riflemen appear to take a greater risk when defending their nest against a more dangerous predator.

It has been suggested that some species may be signalling their intent to attack a nest predator by the intensity of their defence response (Montgomerie & Weatherhead 1988). Gottfried et al. (1985) found that American Robins signal their intention to attack a predator using specific alarm calls. Riflemen, by the intensity of their nest defence response, may be giving an indication of the likelihood that they will attack a predator. Parent Riflemen (5-7g) are insignificantly armed compared to the Little Owl (approximately 180g, Rule 1977) and it seems unlikely that an attack could be successful. However, Riflemen have ignored uneven odds and have attacked me by striking my head and shoulders while I have been banding their chicks. Strikes while I was banding chicks were often preceded by a threat display, in which a Rifleman raised its wings and opened its bill, and down trill alarm calls performed a metre or less from my head. These high risk behaviours may indicate the likelihood of attack by Riflemen. Although unevenly matched, a Rifleman may be able to successfully divert a larger predator's attention from the nest by such an attack.

In conclusion, Riflemen appear to defend their nest more vigorously against predators that pose more risk to themselves, not less risk as predicted by Redondo (1989). Riflemen may indicate the likelihood of attack by a wing raising display and down trill alarm calls.

5. NEST GUARDING BY MALE GREY WARBLERS

INTRODUCTION

I define nest guarding as attentiveness by a parent in the immediate vicinity of its nest in order to defend the nest and its contents against attack. Nest guarding can be carried out by either sex and at any stage of the nesting cycle.

Apparently, most birds do not exhibit nest guarding and the behaviour appears confined to those species at risk from conspecific attack. Moller (1988) found that nest guarding by female and male Colonial Swallows, *Hirundo rustica*, reduced infanticide by conspecifics. Nest guarding by female Eastern Bluebirds, *Sialia sialis*, is likely to be a reaction against conspecific egg dumping (Gowaty et al. 1989). Similarly, the colonial nesting White-fronted Bee-eater, *Merops bullockoides*, remains in the nesting chamber for 65% of daylight hours and 95% of roosting hours during the laying period. It is unusual for any species of bird to remain in the nest before a clutch is complete and this behaviour may counter parasitism by conspecifics (Emlen & Wredge 1986). Male Black-and-White Casqued Hornbills, *Bycanistes subcylindricus*, nest guard their nests against conspecifics due to competition for nest sites (Kalina 1988) and male Gila Woodpeckers, *Meranerpes uropygialis*, spend time guarding the nest from conspecifics rather than foraging or feeding chicks (Martindale 1982). Not all species at risk from conspecific attack or parasitism exhibit nest guarding. For example, conspecific parasitism is common in many duck species but nest guarding has not been observed in this group.

Time spent nest guarding has been found to reduce foraging rates and the size of loads carried to chicks in Gila Woodpeckers (Martindale 1982). A decision must be made by the parent whether to spend time guarding the nest or foraging. Martindale (1982) developed a model to show how foraging behaviour should change as the risk of attack to the nest increases. The decisions on the distance to forage from the nest and the length of time to spend away depend on the probability of the nest being attacked. Therefore, if the probability of the nest being attacked is high, parents should forage closer to the nest and spend only short times away.

While watching Grey Warbler nests during the 1989-90 breeding season at Kowhai Bush I noticed that some male Grey Warblers foraged close to the nest, spent most of their time in the vicinity of the nest, and appeared to be nest guarding. Male Grey Warblers might nest guard for any of the following reasons:

1. Predation is a major contributor to nest failure in the Grey Warbler. In this study, predation rates were 60% in the 1989-90 season and 45% in the 1990-91 season (unpubl. data). Gill (1981) found that 46% of Grey Warbler nests were destroyed by predators over the three year period (1977 to 1979) of his study. Predation in Kowhai Bush is mainly by introduced mustelids (Ferrets, *Mustela furo*, Stoats, *Mustela ermina*, and Weasels, *Mustela nivalis*), and the Ship Rat, *Rattus rattus* (Moors 1983). The Australasian Harrier, *Circus approximans*, Shining Cuckoo, *Chrysococcyx lucidus*, and possibly the Australian Magpie, *Ghymnorhina tibicen*, also contribute to nest predation of passerines.

2. Risk to the nest from conspecifics can take two forms, a direct attack on the nest (Martindale 1982; Kalina 1988; Moller 1988), or parasitism of the nest (Emlen & Wredge 1986; Gowaty et al. 1989). A direct attack on the nest by conspecifics is unlikely to be the main reason for nest guarding in male Grey Warblers. Unmated males have been observed harrassing nesting females on a few occasions (I. McLean pers. comm.; pers. obs.), but they did not cause nest failure. I also consider conspecific parasitism to be unlikely in this species as Gill (1980) checked the contents of Grey Warbler nests daily and did not report finding two eggs in a nest within a 48 hour period (eggs are laid at 48 hour intervals). It is unlikely that risks to the nest from conspecifics have encouraged nest guarding in the Grey Warbler.

3. Grey Warblers are subject to parasitism by the Shining Cuckoo (Gill 1983). The Shining Cuckoo removes one of the host's eggs and replaces it with one of its own. The host's eggs or chicks are smothered or pushed out by the larger cuckoo chick. Shining Cuckoos migrate to New Zealand from their over-wintering grounds in late September to early October. By this time the Grey Warblers have completed most or all of the incubation of their first clutch. Therefore only subsequent nests, either re-nests after predation or second clutches, are susceptible to parasitism by the Shining Cuckoo. Up to 40% of these nests are affected by parasitism (Gill 1981).

I will address the following questions in this chapter:

1. Do some male Grey Warblers nest guard?
2. What are the characteristics of nest guarding behaviour by male Grey Warblers?
3. What are the costs of nest guarding?
4. During which stages of the breeding season (egg-laying, incubation or nestling stage) does the male nest guard?
5. Does the onset of nest guarding behaviour coincide with the arrival of Shining Cuckoos?

METHODS

Data were collected during the 1990-91 breeding season at Kowhai Bush, Kaikoura. Nine first nests and four second nests of Grey Warblers were observed during various stages of the nesting cycle (egglaying, incubation and the nestling stage). While gathering data at Grey Warbler nests, I sat six to eight metres from the nest. First nests were visited every three days for a period of 20 minutes per visit or more. On each visit I recorded whether or not the male was in the nest vicinity. Second nests were visited two to three times daily. As with first nests, the presence of the male near the nest was recorded but only for the first five minutes of the visit. If the male was present, I took an instantaneous sample of his behaviour and recorded his distance from the nest, at one minute intervals for 10 minutes. Behaviours recorded fell into the following categories:

1. Alert perching - bird continuously looked around, often changed perches with small hops.
2. Perching - bird was fairly still, appeared to be resting.
3. Feeding - any successful or unsuccessful attempts to feed.
4. Preening.
5. Flying
6. Vocalisations - included song, sub-song and alarm calls.
7. At nest - included feeding nestlings.
8. Out of sight - bird was obscured by foliage.

I obtained a measure of feeding rate by recording the time between the first and the second peck by the male in the 10 minute sampling period. I recorded the female's presence or absence on the nest during incubation and the number of times the female and male fed nestlings during the nestling stage.

I deemed that the male was nest guarding when less than 10 metres from the nest. Ten metres was chosen as the division between nest guarding and not nest guarding because at this distance it becomes difficult to keep in visual contact with the nest

RESULTS

Male Grey Warblers did not nest guard first nests but did nest guard subsequent nests. Males were not present at 86% of my 86 visits to the nine first nests, observed during incubation and the nestling stage of the first clutch. At 5% of visits the male accompanied the female to the nest and left soon after, and at 9% of visits the male was present only long enough to feed nestlings. At no visit to any first nest did a male stay in the vicinity of the nest for more than one minute so I was unable to sample his behaviour. The four second nests were visited 62 times and all stages were sampled. At these nests the male was present in the first five minutes at 68% of visits and always remained in the vicinity of the nest long enough for me to collect behavioural data.

At the four second nests males spent 86% of the time within 10m of their nests (Fig.5.1). Time budget analysis showed that when males were within 10m of the nest they spent the majority of their time alert perching (56%) and the remainder of their time divided between the other seven categories of behaviour (Fig.5.2).

Males from the four second nests had an average feeding rate of 1.59 pecks per minute ($n=40$) while near the nest.

The mean distance of male from the nest while in the vicinity of the nest was 3.67m (Range 0 - 9m). During incubation the male tended to stay closer to the nest while the female was away feeding ($\bar{x}=3.55$m, $n=90$) than when she was incubating ($\bar{x}=4.46$, $n=131$, Fig.5.3). As only two different males were sampled,

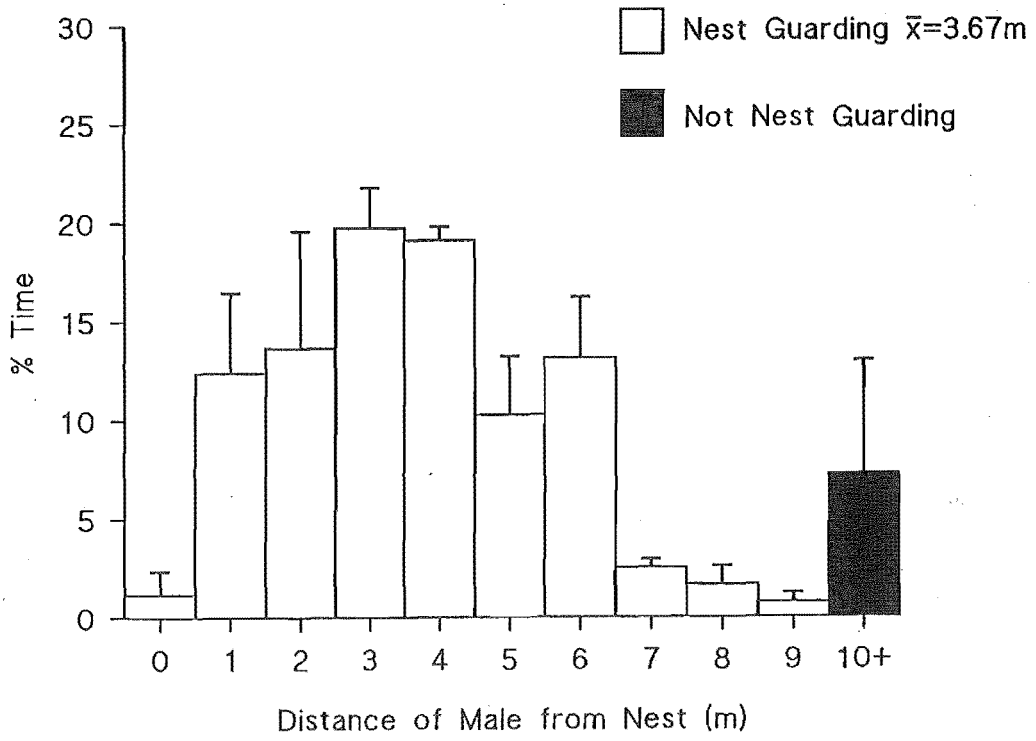

Figure 5.1. Distance of male Grey Warblers from the nest (mean ± SE, n=4). At distances of greater than 10m from the nest the male was deemed not to be nest guarding (see text).

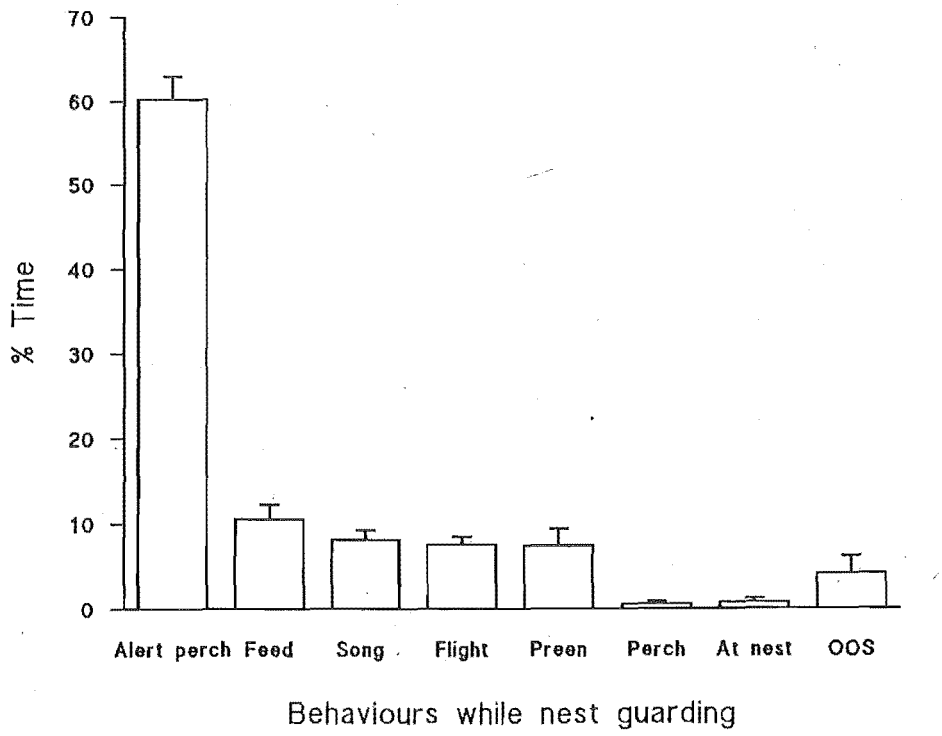

Figure 5.2. Time budget of male Grey Warblers while nest guarding (mean ± SE, n=4).

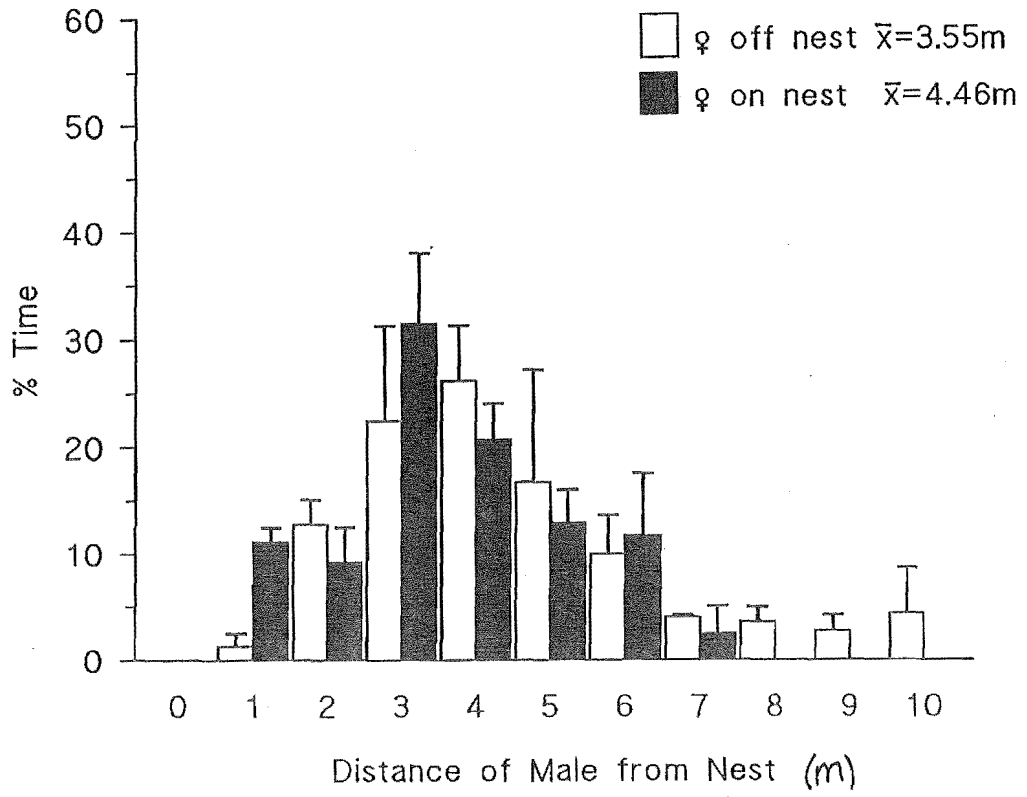

Figure 5.3. Distances from the nest of 2 male Grey Warblers when the female is away feeding, and when the female is incubating (mean ± SE).

sample sizes were too small to test for significance.

Nest guarding was found only at nests initiated after the arrival of the Shining Cuckoos. The first Shining Cuckoo at Kowhai Bush during the 1990-91 breeding season was seen and heard on the 4th of October 1990. By this date first nests contained young nestlings and none of the males from these nests exhibited nest guarding behaviour. Nest guarding was observed at all of the four second nests in which the first eggs were laid during November 1990, well after the arrival of the Shining Cuckoos.

DISCUSSION

Male Grey Warblers appear to guard second nests through all stages of the nesting cycle. All four males from the second nests sampled remained within sight of their nests for most of the time, whereas males from first nests were only rarely seen near their nests.

Characteristics of nest guarding behaviour:

Nest guarding behaviour in male Grey Warblers is characterised by attentiveness at the expense of most other behaviours. This is clearly shown by comparing the behaviour of nest guarding and non-nest guarding males. Cameron (1990), using the same Grey Warbler population and the same time budget methods as this study, found that over all stages in the breeding cycle, males spent most of their time foraging (57%) and only 28% of their time alert perching. The nest guarding males in this study spent only 10.5% of their time foraging, and most of their time alert perching (60%). The data on feeding rates also suggest decreased foraging by nest guarding males. The rate of 1.59 pecks per minute in nest guarding males in this study is less than half that of 3.58 pecks per minute by males found by McLean & Dean (unpubl. data) in the same Grey Warbler population during all stages of the breeding cycle. McLean & Dean's sample and possibly Cameron's (1990) included a few nest guarding males, but they contributed to only a small proportion of the data.

I suggest that foraging rates are lower in nest guarding males due to two factors: (1) Males guarding nests will be watching for predators and so will not be as attentive when searching for prey, and (2) as the male is spending the vast majority of his time in the area of the nest the density of prey items may decrease as he forages, resulting in a lower feeding rate.

The time spent singing by nest guarding males (8%) made this behaviour the third most common behaviour after alert perching and foraging. Singing near the nest could attract predators or the parasitic Shining Cuckoo to the area. However, male Grey Warblers are territorial and sing continually during the breeding season (Cameron 1990). Male Grey Warblers may sing while nest guarding to advertise their territory to conspecifics, despite the risk that it must pose to the nest.

I found that nest guarding males preened more (7%) than the males in Cameron's study (3.5%). Preening is not an attentive behaviour and so must reduce the effectiveness of nest guarding. However, the effect may be small as preening is often for short bursts between periods of alert perching. Perching, also an inattentive behaviour, accounted for only 0.5% of time spent while nest guarding compared to the 7% found by Cameron (1990). This is consistent with the need for nest guarding males to remain alert and attentive as much as possible.

Costs of Nest Guarding:

The requirement for a nest guarding male to remain vigilant results in decreased time available for foraging and territorial defence. My data have shown a decrease in foraging of at least 50% in these males as compared to non-nest guarding males. Regular food intake to maintain a high metabolism is very important in small passerines (Gibbs 1954; Walsberg 1983), and so decreased foraging as a result of guarding the nest may be a significant cost for a male Grey Warbler. Territory boundaries are actively defended by male Grey Warblers during the breeding season. Time spent on maintaining territory is reduced in nest guarding males as they remain in the small area around the nest whereas their territories average 1.14 ha (Cameron 1990)

An almost continuous presence of the male near the nest could reveal the location of the nest to predators. The male's presence near the nest aided me in locating several nests. Singing by the male, sometimes less than 1m from the nest,

must add to the risk of the nest being located by predators or the parasitic Shining Cuckoo.

Benefits of Nest Guarding:

There are several possible benefits of nest guarding behaviour. The greatest risk to nests is that of predation by other species. Up to 60% of Grey Warbler nests have been lost due to predation in a season. Although the loss of nests due to predation is high, I do not consider protection from predation to be the selection pressure behind nest guarding. Nest guarding was observed during daylight hours and the major predators of Grey Warblers (mustelids and rats) are nocturnal. Also, a Grey Warbler weighing about 6g would not have a high success rate when defending its nest against predators. It is unlikely that the benefits gained by defending the nest against these predators would outweigh the costs incurred by nest guarding. Other species in Kowhai Bush also experience a high predation rate but do not appear to nest guard (pers. obs.).

Risk of conspecific attack and brood parasitism have been attributed as selection pressures behind nest guarding in some species. Conspecific attack does not appear to be at a significantly high level in Grey Warblers. The frequency of male harassment of females appears low and nest guarding did not occur during first nests when harassment by unmated males was at its peak. As no cases of conspecific parasitism have been reported for the Grey Warbler, (a detailed study of breeding in the Grey Warbler carried out by Gill, 1980), did not find conspecific parasitism), this is also unlikely to be involved.

I consider the most likely hypothesis explaining nest guarding by male Grey Warblers to be that of reducing parasitism by the Shining Cuckoo. The results show that at nests that have completed incubation before the arrival of the Shining Cuckoo, males do not guard the nest whereas nests initiated after this date exhibit nest guarding. There is a clear relationship between the the presence of Shining Cuckoos and the occurence of nest guarding behaviour.

Why would nest guarding be a useful strategy against parasitism?

A nest guarding male may deter a cuckoo from laying in a Grey Warbler's nest merely by being around the nest site. Cuckoos require secrecy to lay their eggs

(Wyllie 1981), to avoid direct attack from the host and to avoid inducing the host to desert its nest. If a cuckoo did try to either attack or lay in a host's nest then a nest guarding male may be able to repel a cuckoo attack. During the 1990 field season I saw a nest guarding male and its mate successfully repel an attack from a Shining Cuckoo during the incubation stage. The sex of the cuckoo was unclear but the nest was at a stage where it could have been successfully parasitised. Both Grey Warblers chased the cuckoo and the male struck the cuckoo several times. Both birds were alarm calling and this attracted a Fantail, *Rhipidura fuliginosa*, which also mobbed the cuckoo. After about 10 minutes the cuckoo left the area and the female Grey Warbler resumed incubation between 30 minutes and an hour later. This incident shows that Grey Warblers are capable of successfully defending a nest against a Shining Cuckoo.

Are parasitism rates lower at nests with male nest guarders? More data are required before this question can be answered. Nests where males nest guard are still susceptible to parasitism. At least one of the four nests with nest guarding males in this study was parasitised.

Why do other parasitised species not guard nests?

If nest guarding is a successful counter-adaptation to brood parasitism then why is this tactic not widespread among parasitised species? The relationship between a brood parasite and its host can be thought of as a co-evolutionary arms race with both sides developing behaviours to lessen the effect of the other side (Payne 1977; Rothstein 1990). Grey Warblers suffer one of the highest rates of parasitism of any host (Table 5.1) and do not seem to have any obvious counter-adaptations to brood parasitism.

Grey Warblers are egg acceptors, that is they do not seem to be able to recognise a parasitic egg and do not abandon the nest or eject the parasitic egg as some species do (Clark & Robertson 1981; Davies & Brooke 1988; Graham 1988).

Grey Warbler nests affected by parasitism do not produce any host offspring (unless the cuckoo egg is infertile) as the cuckoo chick evicts any eggs or other chicks (Gill 1980). Some parasitic species do not affect the success of their host as much as Shining Cuckoos. For example, the hosts of cowbirds can raise their own young, as well as a cowbird nestling, to fledging. Yellow-hooded Blackbirds,

Table 5.1. Percentage of host nests suffering brood parasitism.

Parasite	Host	% parasitised	Reference
		AFRICA	
Clamator glandarius *C. levaillantii* *C. jacobinus* *Cuculus canourus* *C. solitarius* *C. cafer* *Chrysococcyx cupreus* *Ch. klaas* *Ch. caprius*	43 species	0.5-12.7	Payne & Payne 1967
Chrysococcyx cupreus	5 species	<1	Brosset 1976
		WEST INDIES	
Clamator glandarius	*Pica pica*	43.5	Soler 1990
	Corone corone	8.5	
	C. mondula	2.1	
	Pyrrhocorax pyrrhocorax	4.9	
		BRITAIN	
Cuculus canourus	*Prunella modularis*	1.5	Brooke & Davies 1987
	Acrocephalus scirpaceus	7.3	
	Anthus pratensis	2.2	
	Erithacus rubecula	0.1	
	Acanthis cannabina	0.1	
	Motacilla alba	0.2	
		AUSTRALASIA	
Chrysococcyx basilis	*Acanthiza inornata*	12	Brooker & Brooker 1989
	Malurus splendens	17 - 24	
Ch. lucidus plagosus	*Acanthiza chrysorrhoa*	26	
	A. inornata	8	
Ch. lucidus lucidus	*Gerygone igata*	49	Gill 1980
		NORTH AMERICA	
Molothrus ater	*Vireo solitarus*	48.7	Marvil & Cruz 1989
	Dendroica petechia	41	Clark & Robertson 1981
	Agelaius phoeniceus	7.7	Freeman et al. 1990
M. bonariensis	*A. icterocephalus*	39	Cruz et al. 1990

Agelaius icterocephalus, suffer 40.3% parasitism by the Shiny Cowbird, *Molothrus bonariensis*, but this has a minimal effect on the reproductive success of the blackbirds (Cruz et al. 1990).

Other parasitic species are not restricted to using only one host species. In Britain, the European Cuckoo, *Cuculus canorus*, parasitises six primary hosts (Brooke & Davies 1987), and the Brown-headed Cowbirds are capable of parasitising at least 220 different species (Rothstein 1990). *Ch. lucidus plagosus*, the shining cuckoo in Western Australia, parasitises seven primary hosts - all of the genus *Acanthiza* all of which build enclosed, dome-shaped nests (Brooker & Brooker 1990). The New Zealand race of the Shining Bronze-Cuckoo uses only the Grey Warbler as its host on the mainland. The Grey Warbler is the only relative of the Acanthiza in mainland New Zealand and is the only species to build an enclosed, dome-shaped nest. Being the only suitable host available may have contributed to the high rates of parasitism in the Grey Warbler.

Most species that are subject to parasitism do not seem to suffer such high rates of nest failure as the Grey Warbler, or are not subject to such high levels of parasitism, possibly due to their not being the only host for a parasitic species. These factors may indicate that for many parasitised species nest guarding is too high a cost to pay for the benefits gained. In the Grey Warbler the costs of parasitism may be higher and so the costs incurred by nest guarding are smaller than the benefits. Nest guarding may be a strategy employed by other highly parasitised species that has not yet been described.

In conclusion, although sample sizes are small, the results suggest that nest guarding by male Grey Warblers is an anti-parasitic behaviour, in response to brood parasitism by the Shining Cuckoo. Nest guarding probably has significant costs to the male such as decreased foraging and territorial maintenance, and may attract the attention of predators and even cuckoos to the nest site. Nest guarding may be part of a coevolutionary arms race between the Grey Warbler and the Shining Cuckoo.

FINAL DISCUSSION

Predation accounts for a large proportion of nest failure in many birds, suggesting that nest defence is an important part of parental care in most avian species. The risks taken by parent birds to defend nests can be thought of in terms of investment in their offspring (Trivers 1972). Optimality theory predicts that the pattern of investment in the form of risk taken during nest defence should increase as offspring get older and become more valuable to the parent. This pattern was found in Grey Warblers and Riflemen, as parents defended nests containing nestlings more vigorously than they defended nests containing eggs. However, for both Grey Warblers and Riflemen, the intensity of a nest defence response at nests tested repeatedly decreased through the incubation stage. After hatching nest defence increased throughout the nestling stage for Grey Warblers and, after an initial increase, remained steady for Riflemen. For Grey Warblers, the intensity of the response during the nestling stage increased stepwise in two places; one between days two and five of the nestling stage and the second between days 11 and 14.

The pattern found for Grey Warblers of little change in nest defence nest defence intensity during incubation followed by steped increases during the nestling stage is consistent with predictions of the feedback hypothesis (McLean & Rhodes 1991), which proposes that risk taking by parents will be correlated with the stimulus provided by developing young. However, the pattern found for Riflemen nest defence response does not fit predictions of either the feedback hypothesis or optimality theory, apart from the prediction of both theories, that nest defence will be more intense after eggs hatch.

I found that the level of a parents nest defence intensity to be affected by proximate factors other than the stimulus provided by developing young. Grey Warblers show sexual division of most parental care activities except that both parents feed the chicks, and in this species the male takes a slightly greater risk in nest defence than the female by singing more although all other nest defence measures did not differ between the sexes. Consistent with the high degree of shared parental care by females and males in Riflemen, sex of the defending parent

does not seem to affect the levels of nest defence. The type of predator threatening the nest affects the intensity of a nest defence response. Riflemen responded to a more dangerous predator by taking a higher risk when defending the nest. Some other species have been found to take less risk in defending the nest when faced with a more dangerous predator (Werskal 1979; Elliot 1985). Possibly the parents' response is determined by their perception of the risk posed to the nest, rather than the risk to themselves. This problem requires further exploration.

Previous studies have shown that many other factors can also influence a parents nest defence response, for example parental age (Pugsek 1983), parental experience (Knight et al. 1987), offspring number (Knight & Temple 1986c), offspring quality (Curio et al. 1984; Wallin 1987) and chacteristics of the nest site (Rickleffs 1977; McLean et al. 1986). The influence of some or all of these factors may explain the extensive individual variation of nest defence responses found in studies of nest defence, including mine.

Behavioural strategies appropriate to a particular threat (such as nest guarding against brood parasites by male Grey Warblers) may have developed independently from selection for optimal levels of investment by parents as offspring age. In fact nest guarding should peak during the egg laying and early incubation periods as that is when the threat of brood parasitism is at its height, although nests are vulnerable to predation by the Shining Cuckoo any time until hatching.

It is clear from my data that the methodology used for testing nest defence can influence the results obtained. What is less clear is whether experiments such as these provide a test of the hypotheses purporting to explain nest defence responses by birds. Optimality theory essentially provides a framework for making predictions about how birds should behave. Many proximate factors such as stimuli provided by current young (the feedback hypothesis), type of predator or sex of the responding bird, may be used to refine those predictions in order to more precisely define the likely defensive response in a particular situation.

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APPENDIX 1

Reliability in the recording of flights and hops during model tests.

The number of flights and hops of each parent was recorded during the two minute test period in addition to the measures of distance and call rates. Hops and flights were not used in the analysis of nest defence in Grey Warblers and Riflemen (Chapters 2, 3 & 4) as I considered my recording of them to be unreliable when both parents responded. A comparison of behaviours recorded from tests where both parents had responded to tests where only one parent had responded (regardless of sex), showed that the number of flights and hops were significantly less at tests where both parents had responded (Table A1, Mann-Whitney U test, 2 tailed).

Although the decrease in the number of flights and hops in tests where both parents had responded could be due to having two birds defending the nest as opposed to only one, I cannot rule out the likelihood that I was unable to accurately record the movements of two birds at one time. For this reason the number of flights and hops were excluded from further analysis.

Appendix 1 (cont.)

Table A1. A comparison of the behaviours recorded when both parents responded during a tests to those recorded when only one parent was present in Grey Warblers and Riflemen (Mann-Whitney U test, mean ± SE, NS = $p > 0.1$).

Grey Warbler: Behaviour	1 Parent (n=27)	2 Parents (n=24)	p
Flights (no./min.)	8.66 ± 0.88	4.36 ± 0.65	0.001
Hops (no. /min.)	9.18 ± 0.76	6.48 ± 0.55	0.001
Minimum distance (m)	1.03 ± 0.61	0.92 ± 0.47	NS
Maximum distance (m)	2.73 ± 0.28	2.44 ± 0.94	NS
Mean distance (m)	1.99 ± 0.23	1.69 ± 0.14	NS
Intensity score	3.30 ± 0.23	3.36 ± 0.19	NS
Song (no/min)	2.00 ± 0.67	3.11 ± 0.73	NS
Alarm calls (no./min.)	1 2.85 ± 6.64	8.71 ± 2.65	NS
Rifleman: Behaviour	**1 Parent (n=20)**	**2 Parents (n=28)**	**p**
Flights (no./min.)	10.54 ± 1.02	7.02 ± 0.69	0.006
Hops (no./min.)	13.69 ± 1.03	5.83 ± 0.81	0.0001
Minimum distance (m)	0.79 ± 0.10	1.09 ± 0.13	NS
Maximum distance (m)	2.22 ± 0.16	2.75 ± 0.31	NS
Mean distance (m)	1.47 ± 0.16	2.05 ± 0.20	NS
Intensity score	3.52 ± 0.19	3.08 ± 0.19	NS
Low intensity calls	2.78 ± 0.08	2.83 ± 0.17	NS
Down trills (no./min.)	4.63 ± 2.15	2.42 ± 1.10	NS

APPENDIX 2

Comparison of average nest defence measures from 10 Grey Warbler nests tested repeatedly during incubation and nestling stages (Fig 2.5., Wilcoxon sign rank test, mean ± SE, NS=p>0.1).

Behaviour	Incubation	Nestlings	p
Minumum distance (m)	1.14 ± 0.15	2.12 ± 0.74	NS
Maximum distance (m)	2.77 ± 0.22	2.86 ± 0.22	NS
Mean distance (m)	1.96 ± 0.22	2.16 ± 0.18	<0.05
Intensity score	3.30 ± 0.24	3.16 ± 0.12	NS
Song (no./min.)	3.67 ± 0.80	6.23 ± 1.02	<0.05
Alarm calls (no./min.)	4.99 ± 1.29	1.33 ± 0.67	<0.05

Comparison of average nest defence measures from 9 Rifleman nests tested repeatedly during incubation and nestling stages (Fig. 2.6., Wilcoxon sign rank test, mean ± SE, NS = p>0.1).

Behaviour	Incubation	Nestlings	p
Minimum distance (m)	0.96 ± 0.77	0.92 ± 0.83	NS
Maximum distance (m)	2.39 ± 0.11	2.22 ± 0.16	NS
Mean distance (m)	1.60 ± 0.83	1.40 ± 0.11	<0.05
Intensity score	3.17 ± 0.15	3.54 ± 0.18	<0.01
Low intensity calls	2.79 ± 0.12	2.83 ± 0.12	NS
Down trills (no./min.)	3.09 ± 2.44	6.78 ± 2.43	<0.01

Comparison of nest defence measures from Grey Warbler nests tested only once at either the incubation (n=8) nestling stage (n=5), (Fig. 2.7.,Mann-Whitney U test, mean ± SE, NS = p>0.1, NS = p>0.1).

Behaviour	Incubation	Nestlings	p
Minimum distance (m)	0.76 ± 0.16	0.80 ± 0.12	NS
Maximum distance (m)	2.38 ± 0.28	2.10 ± 0.51	NS
Mean distance (m)	1.67 ± 0.19	1.19 ± 0.16	NS
Intensity score	3.50 ± 0.33	4.00 ± 0.32	NS
Songs (no./min.)	2.63 ± 0.84	7.20 ± 2.08	<0.05
Alarm calls (no./min.)	3.00 ± 2.27	38.20 ± 16.89	<0.05

Appendix 2 (cont.)

Comparison of nest defence measures from Rifleman nests tested only once at either the incubation (n=10) or nestling stage (n=11), (Fig.2.8., Mann-Whitney U test, mean ± SE, NS = p>0.1, NS = p>0.1).

Behaviour	Incubation	Nestlings	p
Minimum distance (m)	0.87 ± 0.15	0.59 ± 0.19	NS
Maximum distance (m)	2.50 ± 0.32	2.23 ± 0.49	NS
Mean distance (m)	1.62 ± 0.20	1.37 ± 0.37	<0.05
Intensity score	3.40 ± 0.22	4.27 ± 0.33	<0.05
Low intensity calls	2.70 ± 0.15	2.81 ± 0.18	NS
Down trills (no./min.)	2.90 ± 1.95	8.73 ± 2.64	NS

Comparison of nest defence measures from Grey Warbler nests tested only once (n=8) or tested repeatedly (n=10) during incubation (Fig.2.9., Mann-Whitney U test, mean ± SE, NS = p>0.1).

Behaviour	Once tested	Repeat tests	p
Minimum distance (m)	0.76 ± 0.16	0.86 ± 0.16	NS
Maximum distance (m)	2.38 ± 0.28	2.38 ± 0.41	NS
Mean distance (m)	1.67 ± 0.19	1.71 ± 0.39	NS
Intensity score	3.50 ± 0.33	3.50 ± 0.38	NS
Song (no./min.)	2.63 ± 0.84	3.00 ± 1.50	NS
Alarm calls (no./min.)	3.00 ± 2.27	19.63 ± 11.43	NS

Comparison of nest defence measures from Riflemen nests tested only once (n=10) or tested repeatedly (n=9) during the incubation stage (Fig.2.10., Mann-Whitney U test, mean ± SE, NS = p>0.1).

Behaviour	Once tested	Repeat tests	p
Minimum distance (m)	0.87 ± 0.15	1.08 ± 0.16	NS
Maximum distance (m)	2.50 ± 0.32	2.61 ± 0.22	NS
Mean distance (m)	1.62 ± 0.20	1.72 ± 0.12	NS
Intensity score	3.40 ± 0.22	3.00 ± 0.17	NS
Low intensity calls	2.70 ± 0.15	2.89 ± 0.11	NS
Down trills (no./min.)	2.90 ± 1.95	3.67 ± 2.81	NS

Appendix 2 (cont.)

Comparison of nest defence measures from Grey Warbler nests tested only once (n=5) or tested repeatedly (n=10) during the nestling stage (Fig.2.11., Mann-Whitney U test, mean ± SE, NS = p>0.1).

Behaviour	Once tested	Repeat tests	p
Minimum distance (m)	0.80 ± 0.12	1.56 ± 0.20	<0.05
Maximum distance (m)	2.10 ± 0.51	2.94 ± 0.27	NS
Mean distance (m)	1.92 ± 0.16	2.38 ± 0.26	<0.05
Intensity score	4.00 ± 0.32	3.13 ± 0.13	<0.05
Song (no./min.)	7.20 ± 2.08	10.25 ± 1.22	NS
Alarm calls (no./min.)	38.20 ± 16.89	2.25 ± 1.58	<0.05

Comparison of nest defence measures from Rifleman nests tested only once (n=11) or tested repeatedly (n=9) during the nestling stage (Fig.2.12., Mann-Whitney U test, mean ± SE, NS = p>0.1).

Behaviour	Once tested	Repeat tests	p
Minimum distance (m)	0.59 ± 0.19	0.94 ± 0.15	<0.05
Maximum distance (m)	2.23 ± 0.49	1.94 ± 0.23	NS
Mean distance (m)	1.37 ± 0.37	1.38 ± 0.15	NS
Intensity score	4.27 ± 0.33	3.56 ± 0.18	<0.05
Low intensity calls	2.81 ± 0.18	2.67 ± 0.24	NS
Down trills (no./min.)	8.73 ± 2.64	7.63 ± 3.98	NS

APPENDIX 3

Differences in nest defence responses of incubating Riflemen to owl, rat and thrush models from Fig.4.2 (Friedmans 2 way ANOVA, mean ± SE, NS = $p>0.05$).

Behaviour	Owl	Rat	Thrush	p
Minimum distance (m)	0.83 ± 0.14	1.04 ± 0.14	1.14 ± 0.14	NS
Maximum distance (m)	2.04 ± 0.18	2.04 ± 0.11	2.58 ± 0.27	NS
Mean distance (m)	1.36 ± 0.14	1.60 ± 0.13	1.74 ± 0.15	NS
Intensity score	2.91 ± 0.15	2.67 ± 0.14	2.42 ± 0.15	0.04
Low intensity calls	2.58 ± 0.23	2.08 ± 0.29	1.5 ± 0.23	0.002
Time to resume inc. (sec.)	384.7 ± 69.4	227 ± 39.7	207.5 ± 37.9	0.04

APPENDIX 4

Time budget of male Grey Warblers (n=4) while in the vacinity of the nest (from Fig.5.2).

Behaviours	% time ± SE
Alert perch	60.25 ± 2.75
Feed	10.55 ± 1.64
Vocalisation	8.17 ± 1.06
Flight	7.64 ± 0.90
Preen	7.43 ± 2.01
Perch	0.54 ± 0.36
At nest	0.78 ± 0.47
Out of sight	8.17 ± 1.06